SEP 18 1925

Vol. 17, No. 3 August, 1925

Medical Lib

PARASITOLOGY

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VOLUME XVII AUGUST, 1925 No. 3

A CONTRIBUTION TO THE LIFE-HISTORY OF A GNATHOSTOME.

BY ASA C. CHANDLER, PH.D.

From the Hookworm Research Laboratory, financed by Indian Jute Mills Association, Calcutta School of Tropical Medicine.

(With 6 Text-figures.)

THE family Gnathostomidae contains several genera and a fair number of species of nematodes of rather aberrant type and of uncertain affinities. As pointed out by Baylis and Lane (1920) in their excellent revision of the family, there is little doubt but that it should be included in the superfamily Spiruroidea. The subfamily Gnathostominae is characterised by the possession of a head bulb containing four closed membranous hollow structures, called ballonets by Baylis and Lane, connected posteriorly with four elongate sac-like structures designated cervical sacs. Three genera are recognised in this subfamily as follows: *Tanqua*, in which the head bulb is provided with transverse cuticular ridges, and *Echinocephalus* and *Gnathostoma* in which the head bulb is provided with rows of thorn-like spines. In *Echinocephalus* the body is smooth and destitute of cuticular spines, whereas in *Gnathostoma* all or a large part of the body has rows of cuticular spines on the posterior edges of the annulations. The first two genera are parasitic in the intestinal tract of cold-blooded vertebrates, whereas *Gnathostoma* apparently has its normal habitat in the stomach wall of mammals, as Baylis and Lane have pointed out.

Although a number of species of *Gnathostoma* have been described only two, *G. spinigerum* from carnivores and *G. hispidum* from pigs, have been adequately described, or have been recorded on more than a single occasion. The other species, except *G. pelecani* and *G. accipitri*, have been obtained from the digestive tract of carnivorous fish or alligators, or have been found in a moribund state in the intestines of mammals, and, as Baylis and Lane have suggested, were probably not parasitic in the host where found, but were ingested with their true, presumably mammalian, hosts. Baylis and Lane did not have access to Skrjabin's (1915) description of *G. accipitri*, found in an eagle in Turkestan, and I too have been unable to consult this paper.

G. pelecani was originally described by Chatin (1874) as *Sclerostoma pelecani*. It is an immature form found in small cysts about 1 mm. in diameter in the subcutaneous tissues and subscapular air sac of a pelican, *Pelecanus onocrotalus*. The cysts in the subcutaneous tissue contain free rolled-up sexually undeveloped gnathostomes, about 3 mm. in length, described as

having four rows of hooks on the head bulb and a body with transverse striations with denticulations, more pronounced toward the anterior end. Baylis and Lane erroneously state that there is no mention of spines on the body. The oesophagus is described as occupying nearly one-half the length of the body, followed by a moderately flexuous brownish intestine with a papillose surface. Three pairs of tubes of unequal size, which are taken to be salivary organs, are said to be present in the cervical region and to open just behind the buccal orifice. Two cysts found in the air sac of this pelican are described as being larger, the contained larvae measuring at least 4 mm. in length, and having begun their sexual development to the extent of the acquisition of a vulvar opening and a whitish moniliform tube which after divers flexuosities reaches the posterior part of the body.

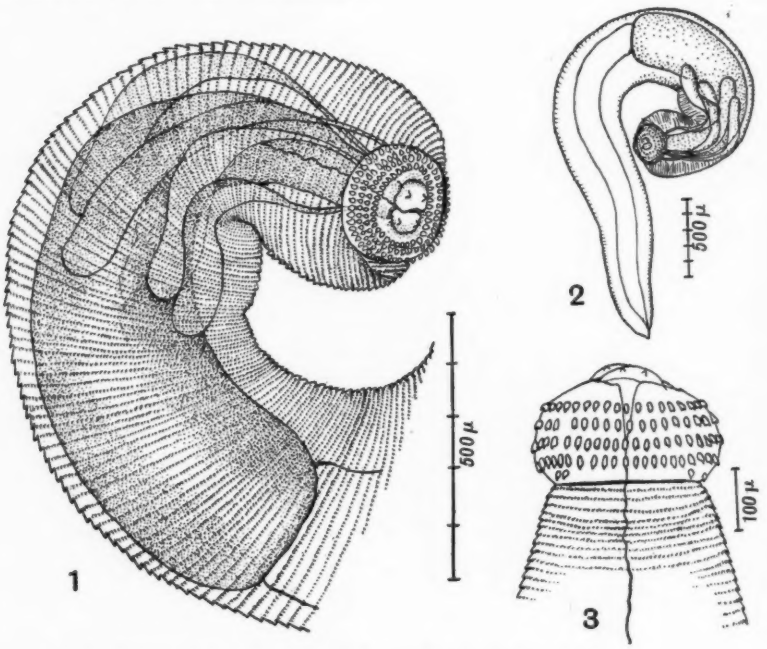

Fig. 1. Anterior end of Gnathostome from cyst in mesentery of cobra.
Fig. 2. Gnathostome from cyst in mesentery of cobra.
Fig. 3. Head bulb and lips of Gnathostome from liver of artificially infected cat.

During the course of the parasitological examination of snakes which died in the Calcutta Zoological Gardens, it was discovered that a high percentage of certain species contained large numbers of small yellow cysts containing gnathostome larvae. These were first found in a Rock Python, *Python reticulatus*, and subsequently in several specimens of King Cobra, *Naja bungarus*, and in well over 50 per cent. of the common cobras, *N. tripudians*. The

cysts were found in the mesentery beginning almost immediately behind the stomach, and in decreasing numbers as the hind gut is approached. In some snakes several hundred such cysts were found.

The cysts are yellow in colour and opaque, spherical, 0·95 to about 1·2 mm. in diameter, with rather thick fibrous walls. Each cyst contains a single rolled-up gnathostome larva varying from 3 to 3·86 mm. in length, and with a diameter of from 400 to 450μ. There are a pair of thick fleshy lips each with two external papillae, and feebly developed interlocking ridges internally,

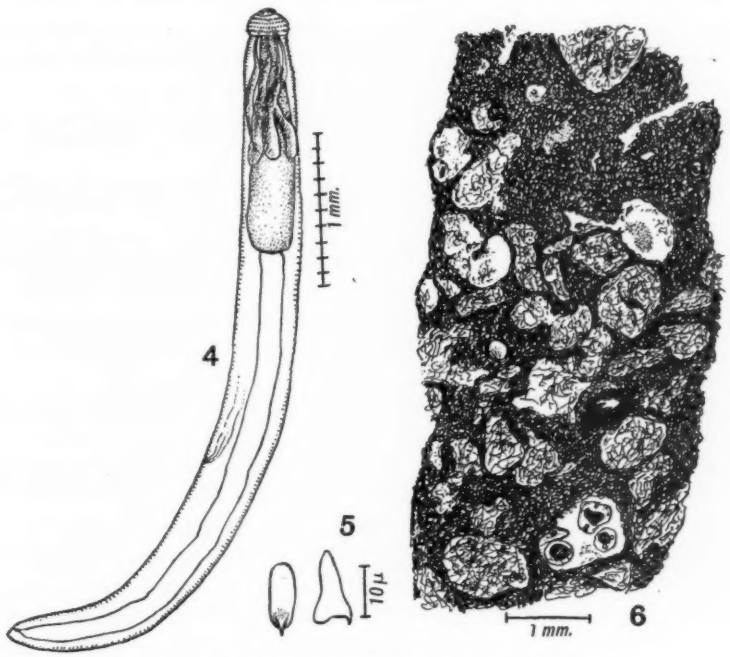

Fig. 4. Gnathostome from liver of artificially infected cat.

Fig. 5. Face and lateral views of hook from head bulb of Gnathostome from artificially infected cat.

Fig. 6. Section of liver of cat showing riddling of tissue by burrowing Gnathostomes. Sections of a coiled worm can be seen near lower edge of section.

similar to those found in *G. spinigerum*. Surrounding the lips and behind them is a conspicuous head bulb about 100μ in antero-posterior diameter and 215μ in transverse diameter. The cuticle is very loosely fitting over the body, so that slight manipulation under a cover glass tends to separate the entire cuticle of the bulb from the body inside. The bulb is armed with four rows of hooks of the form typical of Gnathostoma. Immediately behind the head bulb the body annulations are provided with numerous close-set denticulations, which, as one proceeds toward the caudal end of the body, become gradually

less and less prominent, and finally disappear entirely at about the junction of the middle and posterior thirds of the body. The anus lies near the posterior end, and the tail is short and conical. The oesophagus is simple and club-shaped and of large size, and occupies approximately the anterior $\frac{3}{8}$ of the body. The intestine is brown and its surface has a papilliform appearance. Connected with the head bulb by narrow necks are four cervical sacs of approximately equal length, about 680 to 850μ long, and having the spiral arrangement of fibrils on their walls which is characteristic of these structures in adult gnathostomes.

There can scarcely be any doubt but that these forms are identical with those described by Chatin under the name *Sclerostoma pelecani*. In only one particular does Chatin's description differ from the forms here described from snakes, namely as regards the cervical sacs, thought by Chatin to have been salivary organs. Chatin describes three instead of two pairs of these organs, and states that they are of unequal length. In this Chatin was almost certainly in error. It is significant that when I first examined the gnathostomes from the snake cysts I was uncertain whether there were four or six cervical sacs, but more careful scrutiny and dissection showed that only four were present, and that the lateral portions of the oesophagus visible beyond the external margins of the sacs might readily be identified as an additional pair of sacs. In a few specimens an indication of the development of a vulva shortly behind the middle of the body could be discerned.

The occurrence of the cysts in the mesentery just behind the stomach suggested at once that the embryos had gained access to the snake with swallowed food and had been liberated, presumably from eggs, in the stomach. The striking morphological resemblance in many respects to *Gnathostoma spinigerum*, except in the number of rows of hooks on the head bulb and the simplicity of the body spines, suggested that these larvae might possibly belong to that species. It is conceivable that either in a subsequent moult or by further development of the cuticular structures the number of rows of cephalic hooks might be increased and that with the growth of the worm the annular denticulations might become broader and develop the lateral digitations characteristic of the leaf-like body spines of *G. spinigerum*. Consequently pieces of the mesentery of infected snakes containing numerous cysts were fed to a number of cats, and also to a rat and to two guinea-pigs.

Most of the artificially infected cats died from two to ten days after the feeding, presumably from this infection, since no other cause of death could be found. In every instance large numbers of young gnathostomes, corresponding roughly in number to the number of cysts fed, were recovered from these cats. A number of specimens were obtained from the peritoneal wall lying, often curled up, between the parietal peritoneal membrane and the abdominal muscles, and two or three were found imbedded in the capsules of the kidneys; the majority, however, were found burrowing in the liver tissue. The surface of one or several lobes of the liver was marked by a conspicuous

yellow mosaic marking, reminding one of the marks made on leaves by leaf miners. These were suspected to be, and subsequently proved to be, burrows made by the young gnathostomes. Fig. 6 shows a section of the liver of one of these cats riddled by the burrowing and devouring of the worms. Freshly removed individuals, under the pressure of a cover glass, can be seen to exude a brownish-red fluid from the anus which is undoubtedly semi-digested liver substance. In a few instances gnathostomes were found under the peritoneal lining of the diaphragm, but in no case was there any evidence of their having penetrated this structure, since they were never found anterior to it.

Other artificially infected cats were killed and examined at intervals of one, two, three and four weeks after infection, and living gnathostomes were invariably found in the liver and often in the peritoneal walls. Unfortunately the rat which was fed was attacked and killed, and the viscera eaten, by crows. One of the guinea pigs was killed and examined five days after infection, and while a few of the characteristic mosaic markings on the liver were seen, only a single specimen of gnathostome was recovered, this being in the liver tissue. The second guinea-pig was killed and examined three weeks after infection, but not a single specimen could be found, and there was no evidence of infection having occurred.

The burrowing gnathostomes recovered from these artificially infected animals closely resembled those removed from the snake cysts, but were larger and had evidently undergone some further development. The worms removed from cats which died two days after infection varied in length from 4 to 5·6 mm., with a diameter of from 400 to 560μ, whereas specimens obtained from a cat which died 11 days after infection measured from 6·2 to 6·85 mm. in length by from 525 to 575μ in diameter; they were, therefore, relatively longer and slenderer than the encysted forms. The oesophagus and cervical sacs had not grown in proportion to the body length, the former occupying from 27 to 33 per cent. of the total length. At a point about 60 to 65 per cent. of the length of the body from the anterior end a well-developed vulva was present in some specimens and not in others, representing the beginning of the development of the female reproductive organs. From the vulva a tube could be traced forward (not backward as described by Chatin) for an indefinite distance. The specimens which lacked any trace of a vulva and which were presumably males, had a somewhat shorter tail than the females, but no caudal alae or papillae or any part of the male reproductive system was yet in evidence.

Gnathostomes recovered from cats killed two, three and four weeks after infection showed no further development either in size or structure than did some specimens obtained six days after infection.

On the post-mortem examination of cats which had been used for other purposes, and which had not been fed on material from snakes, about 10 per cent. were found which were naturally infected with immature gnathostomes identical in every respect with those found in the artificially infected cats;

from three to as many as 25 specimens have been found in these animals. As in the artificially infected cats, the gnathostomes were found in the liver and in the walls of the peritoneum. The liver invariably shows the characteristic burrow marks, and it is always possible by a mere superficial inspection of the liver to say whether or not a cat is infected. In only one of these naturally infected cats was a gnathostome tumor found in the stomach wall; this contained a single male, not quite adult, with the cephalic spines and cuticular scales typical of *G. spinigerum*. If the forms found in the liver and the adults in the stomach of cats are the same species, it seems evident that the morphological changes take place by means of a moult and not by gradual development.

The significance of the findings recorded above is entirely problematical. Several interesting hypotheses present themselves, but all of them are largely speculative. In the first place, are the larval forms here described stages in the life-cycle of *Gnathostoma spinigerum* or of some still undiscovered species? *G. spinigerum* occurs as an adult in tumours in the stomach wall of carnivorous mammals, especially tigers, leopards and cats, and has several times been recorded in an immature state in the subcutaneous tissue of man; the latter shows evidence of a tendency to burrow, the parasites apparently having strayed and wandered to an unnatural habitat in an abnormal host. It has been found to be a fairly common parasite of domestic cats in Calcutta during the summer months, but since the cysts were discovered in the snakes in October, up to early March, no more infected cats have been found except the one described above. It is possible that this indicates a seasonal incidence of the infection, in which case the infected cats must die since the tumours could not possibly heal in so short a time, or it may be that the source of supply of the cats has happened to be a district of the city where opportunity to acquire the infection has not been present.

Usually only one cyst is present in the stomach wall, this harbouring from one to nine gnathostomes, but as many as three tumours have been found. The connection with the lumen of the stomach is sometimes almost vestigial, only a very narrow canal being present, whereas there is frequently a similar minute canal leading into the body cavity. The species was originally described from a captive tiger in which it had produced a fatal perforation of the stomach wall. The worms produced eggs which contain developed embryos, but these eggs cannot always be found in the faeces or intestinal contents of infected animals.

Nothing is known of the life-cycle of this or any other member of the genus *Gnathostoma*, but the larvae of a species of the allied genus *Echinocephalus* have been found encysted in the tissues of the pearl oyster, *Margaritifera vulgaris*, which is looked upon as a normal intermediate host, since the adults occur in oyster-eating fishes. In this case the arrangement of the spines on the head bulb is the same in the larvae as in the adult. Not more than one larva has been found in any one oyster. In all of the Spiruroidea in which the

life-cycle is known the eggs escape by the intestinal route and then undergo development in another host where they commonly encyst, finally reaching the definitive host when the intermediate host is devoured. If we assume for the moment that *Gnathostoma* has a life-cycle of this type, then to explain the massive infection found in snakes, since snakes are not coprophagous, we would have to conclude that the eggs contained in the intestinal contents, in the verminous tumour, or in the worms themselves, still inside the definitive host, must be the source of the infection in the intermediate host; whether or not the larvae in the snakes are *G. spinigerum* it appears probable that we are dealing here with a species of *Gnathostoma* in which such a means of transfer to the intermediate host can occur, and if in one then quite possibly in all. But while such an explanation would account for the infection in a python, which may quite possibly include cats in its bill of fare fairly frequently, it is certain that cobras do not indulge in a cat diet to such an extent as to make a 50 per cent. infection possible. We are driven, therefore, to conclude either that there is a preliminary intermediate host which is coprophagous or carrion-eating and which is then eaten by the snake, or that the larvae in the snake do not represent *G. spinigerum* at all, but some undescribed species from a smaller animal. As regards the former alternative, the case would be unique in nematode life-histories unless we should further assume that the development in cysts in snakes is not a normal part of the life-cycle at all, but an instance, like the occurrence of immature gnathostomes in man, of development in an accidental and abnormal host. It is known, for instance, that the larvae of *Spirocerca sanguinolenta* occur in encysted form in many cold-blooded vertebrates which have chanced to feed on infected insects, but this occurrence does not represent a normal link in the chain of events in the life-cycle of this worm. However, the frequency of the infection in snakes, and the regularity of the development up to a definite stage, together with the subsequent release and further development when swallowed by a carnivore, make it difficult to believe that we are not dealing with a normal part of the life-cycle. As regards the latter alternative, that the larvae represent an undiscovered species, the only contrary argument is the frequency of the infection in snakes and the surprising fact that the adult of such a common nematode, especially if a mammal parasite, should never have been met with and described. A further difficulty presents itself; since the encysted larvae occur in large numbers in the infected snakes, one would expect that the definitive host, after feeding on such a snake, would develop a massive infection. In cats the maximum number of *G. spinigerum* so far found in a single host has been nine, and usually not more than two or three are present. The mechanical damage done to the liver of cats by the larval gnathostomes, and the mortality apparently caused by the ingestion of only a fraction of the cysts contained in a snake, make it difficult to understand how a smaller vertebrate, such as might commonly be devoured by cobras, could withstand a massive infection. The occurrence of the same larval gnathostome in a pelican, and possibly in an

eagle, if *G. accipitri* is the same species, might be accounted for by assuming either the swallowing of the definitive host or a small intermediate host, or of infected snakes and the liberation and subsequent re-encystment of the worms. It is easy to suggest possible hosts which might become infected by eating snakes, and also to suggest other hosts which might serve as a source of infection for the snakes, but no entirely logical suggestion has yet occurred to me which would account for the transfer back and forth between snake and definitive host. It is hoped that opportunities will come for solving this unusually interesting problem. In the meantime the larval worms found encysted in snakes, and burrowing in the liver and peritoneal walls of cats, must be known as *Gnathostoma pelecani* (Chatin).

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(*MS. received for publication* 30. III. 1925.—Ed.)

LERNAEA (*LERNAEOCERA*) *ELEGANS* N.SP., A PARASITIC COPEPOD OF *ANGUILLA JAPONICA*.

By W. HAROLD LEIGH-SHARPE, M.Sc. (Lond.).

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Lecturer in Biology, St Mary's Hospital Medical School, Paddington, London, W.

(With 5 Text-figures.)

Habitat and Record. During November 1924, by the courtesy of Seizo Takeda, I received from the Yogyo Shikenjyo (Piscicultural Experiment Station) at Kitajima near Toyohashi, Japan, the head of a small Japanese eel, *Anguilla japonica*, whose buccal cavity appeared to be completely filled with about forty parasites belonging to the genus usually known as *Lernaeocera*, but to which Wilson (1917, p. 3) has given reasons for restoring the name *Lernaea* Linnaeus. (See Note, p. 251.)

The history of *Lernaea* (*Lernaeocera*) in England, as given by Scott (1913, p. 155) is very interesting, since both species seem to have disappeared from this country, no author having recorded them since Barbut (1783). The specimens from Japan differ very widely from these species (*L. cyprinacea* and *L. esocina*), but approximate more closely to *L. lagenula* Heller 1865 from an unknown host in Brazil, but from which they differ in having a more elongated neck, and from all species by the auricular expansions of the head, so that for the Japanese specimens I propose the name *Lernaea elegans*. I believe this is the first parasitic Copepod to be recorded from *Anguilla*, and certainly the first Asiatic species of its genus.

The buccal cavity of the eel is only 17 mm. in length and 10 mm. at its broadest part, and so crowded with parasites that it is wonderful that the fish could swallow any solid food. The parasites are so deeply embedded, in the jaws reaching to the bone and one even on the tongue, that they are exceedingly difficult to remove intact; and, because they were so much more buried than I expected, I only succeeded in removing four large ones undamaged. Digging them out is of no avail, but the impenetration of a needle followed by a rapid flicking movement, so that the anterior end is jerked out, proved the only successful method. As indicated in Fig. 1, all that part of the animal above the transverse dotted line lay embedded beneath the skin of the host. Immediately upon emergence from the tissues the animal is bent at an angle of 135° or more, standing then perpendicularly to the jaws; in Fig. 1 the animal is represented straightened out as it is mounted on a slide, but the posterior

part of the trunk which projects dorsally is turned towards the (spectator's) right so that there is a twist in the hinder part of the animal's neck just below the dotted line. No part of the animal exhibits any traces of segmentation.

Body. The outline of the body is best seen from Fig. 1. The total length of one of the, if not the, largest specimen is 8·7 mm., of which the cephalothorax (head and neck) occupies 3·5 mm., the trunk 3·4 mm. and the ovisacs 1·8 mm. The animals are of a bright chlorophyll green colour. Under the microscope this is found to be due to large hollow spherical masses, which are so numerously distributed throughout the coelom as to completely obscure

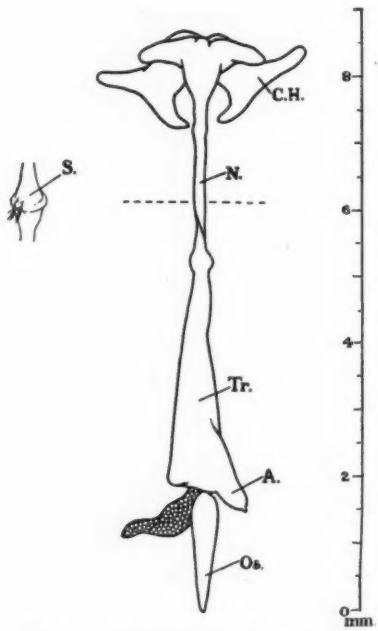

Fig. 1. *Lernaea elegans* ♀. The entire animal in ventral aspect mounted on a slide in Farrant's medium. C.H. = cephalic horns; N. = neck; S. = enlarged base of neck; Tr. = trunk; A. = abdomen; Os. = ovisacs.

the internal anatomy, composed of a transparent matrix in which are embedded numerous minute spherical green bodies. I suggest that these are symbiotic algae of the Volvocales type which may have lost their flagella, but in any case are not well enough preserved to exhibit any. The only parasite taken from the angle of a gill slit did not contain these algae.

The *Head*, which is ovoid, bears anteriorly a spherical apex from which arise the appendages, and at the summit of which is the mouth. From the outer edges of the ovoid spring the four lateral *cephalic horns* (Fig. 1, C.H.) the usual bluish chitinous organs of fixation of the Lernaeidae. These stand

foursquare like a letter X at right angles to the neck resembling the petals of a flower outspread. The ventral pair is simple and unbranched. The dorsal pair is nearly twice as broad (the two horns taken together), having an extreme width of about 3·4 mm. and each ramus is bifurcated, resembling in this respect, as far as I can make out, *L. temnocephala* Cunnington 1914, but in the largest specimens only. I do not think that it has been noted in other species that the posterior pair is not bifurcated in the younger specimens. In Figs. 1 and 2 the dorsal pair is doubled under in mounting. Each side of the globular portion of the head is expanded laterally into a muscular, leaf-like projection, rolled with its concavity facing anteriorly, and recalling in appearance the appendix of the auricle of a rabbit's heart. I have called these the auricular expansions, and I do not find them recorded in any other species. They are between the pairs of horns.

The *neck* is long, slender and elegant, even longer than in *L. lagenula*, and in great contrast to that of *L. cyprinacea*. At the posterior end, where it joins

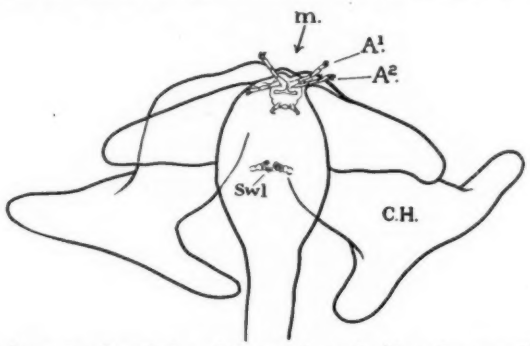

Fig. 2. *Lernaea elegans* ♀, enlarged view of the anterior end under a low magnification. C.H. = cephalic horns; m. = mouth; A^1. = first antennae; A^2. = second antennae; Sw. 1. = first pair of swimming legs.

the trunk, it is enlarged as in *Medesicaste* and *Peniculus clavatus*. This also is a specific character.

Appendages. (Fig. 3. The appendages on the spectator's left are probably more perfect.)

The 1*st Antennae* (A^1.) are four-jointed, the basal joint fused with the head and the longest, the joints decreasing in size. The third joint bears a thumb-like projection covering the base of the fourth joint which ends in three finger-like processes and, in some specimens, a fourth thumb-like one. There are now no setae present on these joints.

The 2*nd Antennae* (A^2.) are three-jointed, strongly setigerous, a spine-like long seta rising at the base of the second and third joints. The antenna ends in three finger-like processes apparently cut off as fourth joints of equal value.

The 1*st maxillae* (1 m.) I am unable to make out clearly, but each appears to end in a single claw.

The 2*nd maxillae* (2 m.) consist each of a stout base which merges into the auricular expansion, and terminates in two moveable claws which meet the two of the other side on the median line and point upwards (by the overlapping of the claws only one claw is shown on the right of Fig. 3).

The *mandibles* (Mn.) are contained in large sacs and are curved and styliform. Without teeth in other species they are probably in the same condition in this.

The *maxillipedes* (Mp.) are large, two-jointed, the distal joint being convex posteriorly on the inner side, terminating in two mammillated spines and two fine spines, and capped by three two-jointed claws of equal value, the outer being the larger, and two mammillated spines.

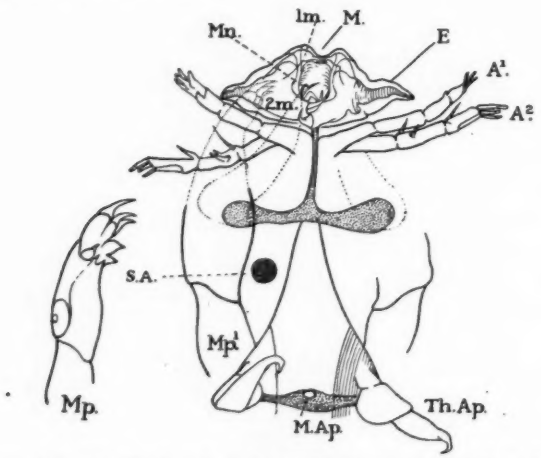

Fig. 3. *Lernaea elegans* ♀. Head under a high magnification, the cephalic horns not shown. M. = mouth; E. = auricular expansions; A^1. = first antennae; A^2. = second antennae; 1 m. = first maxillae; 2 m. = second maxillae; Mn. = mandible and sac; Mp. = maxillipede; Mp^1. = base of maxillipede *in situ*; S.A. = one of the numerous symbiotic algae; Th.Ap. = first pair of thoracic appendages; M.Ap. = median aperture, possibly excretory. The stippling indicates chitinous portions.

There is a single pair of *thoracic appendages* (Th.Ap.), three-jointed, the terminal joint being uncinate. They are non-setigerous and cannot be called swimming legs. Between the basal joints of these appendages appears what I consider a single median aperture, which may be that of the renal excretory organs though Wilson (1917) states that *Lernaea* possesses none.

The **Trunk** (Fig. 1, Tr.) is narrow and slender, terminating in a dome-like bluntly rounded abdomen which projects as a keel. The pregenital prominence is hemispherical, and just behind it emerge the ovisacs which are fusiform, moderately long and tapering, and contain many rows of numerous eggs (Fig. 1, Os.). The abdominal appendages on either side of a well-marked anus take the form of caudal styles (Fig. 4, C.S.). These consist in the immature

forms (*i.e.* those bearing no ovisacs) each of a minute two-jointed base (the terminal joint bearing one seta on its outer side) surmounted by an extremely long seta, of which I have only three perfect specimens (Fig. 4). In animals a trifle larger the seta is broken off at a constriction near its base, while in the larger specimens, the great majority, only the base is left. To the posterior end of the trunk are in a few cases attached some epizoic Vorticellids, also noticed by Cunnington (1914) in African species.

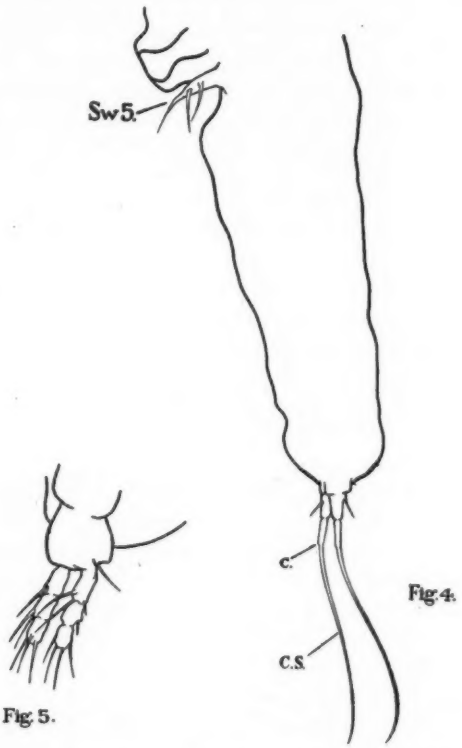

Fig. 4.

Fig. 5.

Fig. 4. *Lernaea elegans* ♀. The posterior end of the trunk under a high magnification. C.S. = caudal styles; c. = constriction in seta; Sw. 5. = fifth pair of swimming legs.

Fig. 5. *Lernaea elegans* ♀. The third pair of swimming legs under a high magnification.

I have been able to find all the pairs of **swimming legs** so characteristic of the African species, Cunnington (1914, Lake Tanganyika), Wilson (1924, White Nile). The appendages homologous with the *first pair* (Fig. 2, Sw. 1) are a good distance posterior to those which I have already stated, are uncinate and non-setigerous in *L. elegans*. The *second pair* occurs on a slight swelling at the anterior end of the neck, indicated in Fig. 1. The *third pair* (Fig. 5), which is markedly larger than the second, and which it resembles, is situated

on the large swelling at the base of the neck. A ring-like band marks the origin of both pairs. Each appendage is biramous and strongly setigerous, each ramus consisting of three joints inserted on a hemispherical common base which exhibits curious details. This pair is the most easily seen.

The *fourth pair* is situated at the anterior end of the trunk; their presence is indicated but I am unable to make out the details. They are similar and biramous. The *fifth pair* (Fig. 4, Sw. 5) is represented by two one-jointed stumps just in front of the vulvae. Each stump bears two lateral setae and terminates in a long seta. The basal joint, of the first pair of swimming legs, bears an incurved process towards the middle line.

The **alimentary canal** is on the same general plan as in *Peniculus clavatus*, being much enlarged in the head-region (Fig. 3) and having two small dilatations corresponding to the swellings on the neck. There are two rows of saccate caeca along the greater part of its length even in the neck, as in Nordmann's figure of *L. esocina* (quoted by Scott, 1913, Plate L, fig. 1, as *L. cyprinacea*), similar to the single row described in *Peniculus* by Leigh-Sharpe and Perkins (1924).

I do not feel in accord with these investigators who consider that the configuration of the cephalic horns is of the greatest importance in the diagnosis of species. I observe that this character depends upon (*a*) the age of the individual, (*b*) approximation in growth to some barrier, *e.g.* the jawbone, which may retard or inhibit development. Thus the configuration may lead to grave errors where only a few specimens are available for examination. For instance, in *L. elegans* I find:

(1) The dorsal horns are only bifurcated in the few specimens of more than average size.

(2) One horn of the dorsal pair may be slightly bifurcated, and the other not at all. (If the ventral pair be absent, an asymmetrical three-horned head would result, such as is alleged to exist in *L. catostomi* Krøyer.) This occurs in most specimens of average size.

(3) One horn of each pair may be fully developed, the other horn of each pair being but half the size. In a section of a piece of the eel's head this inequality is seen to be due to contact with a neighbour or with a bone.

(4) Various cases of asymmetry.

The knowledge I have acquired of these animals leads me to the conclusion that in the most degenerate families (numbering three or four) of permanently attached parasitic Copepoda the appendages most liable to variation, and occasionally the only ones, are the maxillipedes, the ones retaining the most, yet slightly-varying functional exercise, as is plainly demonstrable, *e.g.* in the various species of *Lernaeopoda*, and that no collector should be satisfied that he has identified a species, and no investigator should erect a new one, until he has examined the maxillipedes. For the same reason observation of the mandibles is important, but they are not so easily detectable.

Specific characters ♀. The dorsal pair of cephalic horns in old specimens

is bifurcated and nearly twice as wide (in a flattened preparation) as the ventral pair. Head with lateral auricular expansions. Neck very long and slender, with a posterior swelling where it joins the trunk. The bases of the 2nd and 3rd joints of the 2nd antennae are provided with a strong spinous seta. The maxillipedes are characteristic (*vide* text). A first pair of thoracic appendages is non-setigerous and uncinate; this pair has been overlooked by all other investigators *if* it occurs in other species. The first pair of swimming legs is some distance posterior to this pair, and the basal joint of each leg bears a small distinct process incurved towards the middle line.

Host: *Anguilla japonica*.

Suggested name for the symbiotic alga: *Cassatiovolvox copepodicola*.

My thanks are due to Miss Edith C. Humphreys for the great pains she has taken in reproducing the figures.

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NOTE.

Since this paper went to press, Mr Yoshiichi Matsui, Director of the Experiment Station, informs me that the parasite was first discovered during the summer of 1922 in a fish cultural pond near the Kitajima station. This pond, measuring about one hektare, yielded only about 300 kilogrammes of eels bearing Copepods, but the parasites have gradually become widespread, and now (March 1925) are found commonly in the fish-rearing ponds of Central Japan (Aichi, Shizuoka and Miye provinces).

Besides occurring on eels the Copepods are found as ectoparasites upon the scales of *Cyprinus carpio* L., *Carassius auratus* (L.) and *Pseudorasbora anguillicaudata* (Cantor). They occur almost exclusively in fresh water; their presence in brackish water is rare.

All the specimens from *Cyprinus carpio* received by me are white and devoid of symbiotic algae.

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(*MS. received for publication* 6. III. 1925.—Ed.)

ON THE LIFE HISTORY, MORPHOLOGY AND SYSTEMATIC POSITION OF *APELMA* KIEFF. AND *THYRIDOMYIA* N.G. (DIPTERA, NEMAT. CERATOPOGONINAE).

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(*From the Molteno Institute for Research in Parasitology, University of Cambridge.*)

(With Plate VII and 9 Text-figures.)

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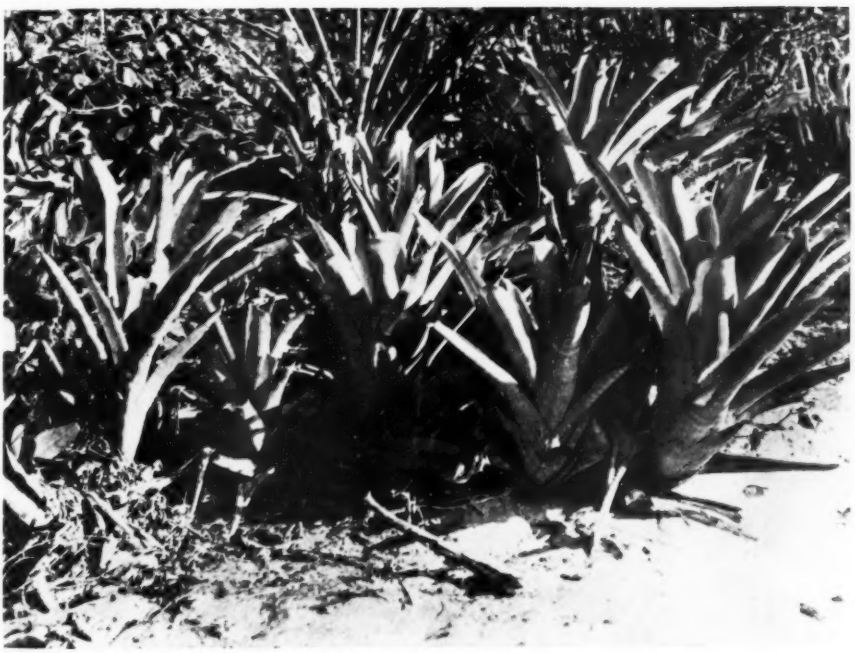
GENUS **APELMA** KIEFFER 1919.

The genus *Apelma* was erected by Kieffer (1919) for the inclusion of two European species, of which he had males only. The characters upon which he laid stress, and by which he separated the genus from *Forcipomyia*, were the length of the claws and the absence of an empodium. Nothing is known of the early stages of these two species. Subsequently, Ingram and Macfie (1923) described an African species from three males reared by Bacot from larvae in the leaf axils of *Dracaena* sp. The early stages of this species were not preserved.

In 1923[1] the writer found larvae of five distinct species living in terrestrial Bromeliads of the genus *Aechmea* (Plate VII) growing on the rocks and islands of Rio Bay, Brazil, and on the sandy soil of Pernambuco some miles inland.

[1] The writer was a member of the Cambridge Zoological Department Expedition to Brazil in 1923.



Terrestrial Bromeliad plants of the genus *Aechmea* in which the early stages of *Apelma* spp. were found; photograph taken near Rio de Janeiro, Brazil.

Adults reared from these larvae were readily identified as *Apelma* spp. by the absence of empodia in the males, and by the characteristic H-shaped internal chitinisations of the male hypopygium (cf. *A. bacoti* Ingram and Macfie, 1923). Females of the genus now obtained for the first time disclosed an interesting case of sexual dimorphism, this sex possessing well-developed empodia (Saunders 1924 *b*). Kieffer's generic diagnosis, therefore, applies only to the males. The females, in common with those of *Thyridomyia*, may be distinguished from those of *Forcipomyia* by the strongly compressed basal flagellar segments of the antennae.

Habits of Early Stages.

In view of the terrestrial habitat of all closely related Ceratopogonines it is interesting to note that the immature forms of *Apelma* are strictly aquatic. The larvae are notably flattened dorso-ventrally, a modification which enables them to exist in the capillary water between the closely appressed leaves of Bromeliads even when the main supply is spilt by the chance overturning of the plant. They seem to live normally in these spaces, for scarcely any larvae are dislodged if the water is poured out, but many will be found when the leaves are removed one by one. Pupae and mature larvae occur commonly between the outer leaves, and younger and younger larvae appear as the heart of the plant is approached, pointing to the centre as the favourite site for oviposition. The ability to live in such narrow confines serves the further purpose of concealment from the predaceous enemies which abound in Bromeliads. (In addition to the well-known Odonate nymphs *Mecistogaster*, the larvae of Megarrhine and Culicine mosquitoes, and the Coleopterous larvae that have been recorded from Bromeliads, the writer found a Tanypine larva (Chironomid) but was unable to rear it; this constitutes a new record for the fauna of Bromeliad plants.)

Until more larvae have been discovered it will be impossible to decide whether the flattened condition is characteristic of the genus or merely a secondary adaptation to the very specialised mode of life. It is highly probable that the larvae of *A. bacoti* are also flattened, since they were found living under similar conditions. Calvert (1911) has advanced the hypothesis that life in Bromeliads induces a flattening of the body, and cites a Coleopterous larva and a Hemipterous nymph as examples. Dr H. Scott (Bolivar, 1924) records a similar instance of the flattening influence of such environments on the cockroach *Hololeptoblatta* living in *Pandanus* in the Seychelles.

Morphology.

All species were separated in the early stages with the unaided eye or with the use of a hand lens; later microscopic examination revealed very few additional characters either in the larvae or pupae. While of a type peculiarly their own, the larvae show affinities with *Thyridomyia*, and clearly fall within that series of genera whose adults have well-developed empodia, namely

Atrichopogon, *Thyridomyia* and *Forcipomyia* (*Lasiohelea* and *Microhelea* are not yet known in the early stages).

The morphology is here discussed in detail, and only those characters which are of specific importance will be mentioned in the description of species.

Larva.

Head. The head is the most variable structure in this genus, affording practically the only macroscopic means of separating the species. It may be

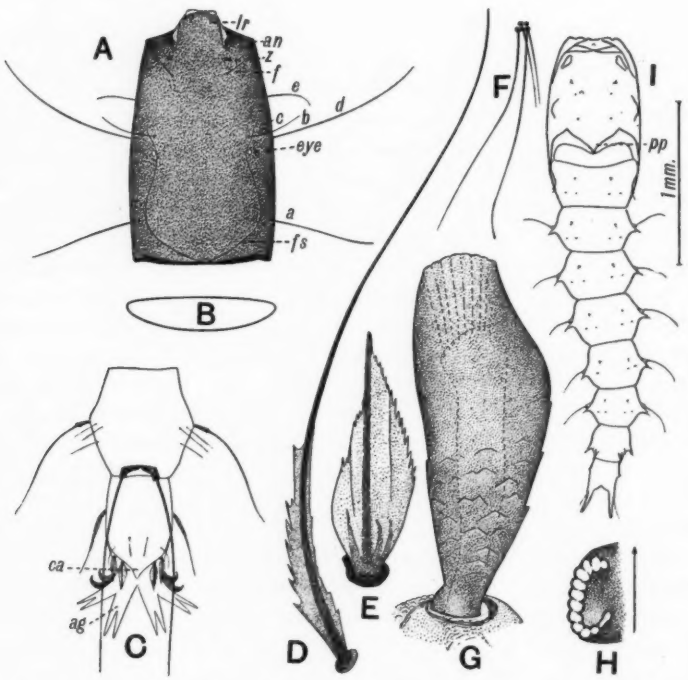


Fig. 1. *Apelma edwardsi* n.sp. Larva: **A**, dorsal view of head. **B**, cross section of head. **C**, dorsal view of extremity of body. **D**, lateral "finned" hair from abdominal segment. **E**, blade-like modified hair from tip of abdomen. **F**, latero-ventral thoracic group of sensory hairs. Pupa: **G**, outer view of left prothoracic horn. **H**, tip of left prothoracic horn. **I**, dorsal view of entire pupa. *Lettering: ag* = anal blood-gills; *an* = antenna; *ca* = cauda; *fs* = frontal suture; *lr* = labrum; *pp* = posterior median prolongation of thorax; *a–f* = hairs of head; *z* = sensory pit.

short and broad, or long and narrow; colourless, or heavily pigmented. It is always strongly compressed dorso-ventrally (Fig. 1, B) and is in the same axis as the body, not directed downwards as in allied genera.

The Frontal Suture (Fig. 1, A, *fs*) is distinct on the posterior part of the head, but is lost after passing inside the eyes and outside the *b* hairs.

The Eyes (Fig. 1, A, *eye*) consist of an inconspicuous clear spot in the chitin of the upper surface of the head, beneath which may be seen the usual bilobed mass of black pigment.

The Antennae (Fig. 1, A, *an*; 2, D) are very small discs set in an opening in the chitin on the anterior angles of the head; in each there are two small membranous areas bearing minute sensory processes. In some species the central portion is slightly raised, suggesting a rudimentary cylindrical process. It will be seen at once that this constitutes a very radical change from the long slender antennae of *Atrichopogon* and *Forcipomyia*; larvae of *Thyridomyia* recently discovered by the writer exhibit an intermediate stage, where the antennae have migrated part-way down the front of the head, and are almost as much reduced as in *Apelma* (Fig. 7, D, E, I). The character forms a connecting link with those Ceratopogonines whose larvae are of the slender, vermiform type (*Dasyhelea*, *Bezzia*, *Culicoides*, etc.).

Chaetotaxy (Fig. 1, A; 2, B, E): there are a number of simple slender hairs and a few sensory pits regularly disposed upon the head; these are unchanged in all the species discussed. Those which can be homologised with the hairs and pits of the larval head of related groups are as follows: the closely associated long and short hairs *h* at the sides of the mouth as found in nearly all Ceratopogonines (not *Forcipomyia* s.str.); the solitary pair *w* placed further forward which occurs in all genera examined; the pair *y* on the ventral surface; the dorsal sensory pit *z* behind the lateral posterior limits of the labrum, which seems to be present in all Ceratopogonines; and the lateral anterior sensory pit *a* which was made ventral by the flattening of the head. The remaining hairs on the dorsum and sides have been given an arbitrary lettering *a–f* for future use if desired.

The Mouth-parts: the opening in the head capsule to accommodate the mouth-parts is sub-elliptical in shape, and occurs entirely on the ventral surface. The margin of the aperture is strongly reinforced with chitin.

The Labrum (Fig. 1, A; 2, B, C, *lr*) consists of a chitinous median prolongation of the dorsal surface of the head, and a fleshy portion beneath, which extends downwards and backwards as a narrow ridge between the maxillae, eventually forming the roof of the mouth cavity and joining the transverse bridge of the hypopharynx. Paired sensory organs occur on the anterior extremity of the fleshy portion (*epipharynx* of some writers), and at intervals on the ventral surface; this region is also clothed with fine hairs along the median ridge.

The Premandibles occur beneath the dorsal chitinous portion of the labrum; they are very short, and each is divided into two separate pieces as in *Dasyhelea*. Insufficiency of material has prevented the complete elucidation of the arrangement and action of these interesting organs.

The Mandibles (Fig. 2, B, C, *md*) are very unusual in form. They have a large hollow basal portion which tapers sharply into a long slender shaft terminating in two teeth; near the middle the shaft is bent abruptly to an angle of nearly

90°. A fringe of short hairs lines the side of the slender distal portion. The mandible hinges on a process arising from the side-wall at the anterior corner of the head, and the large basal portion is accommodated in a special *mandibular chamber* (Fig. 2, C, *mch*) with a thinly chitinised roof continuous with the membrane of the labrum. The bend in the mandible permits the distal

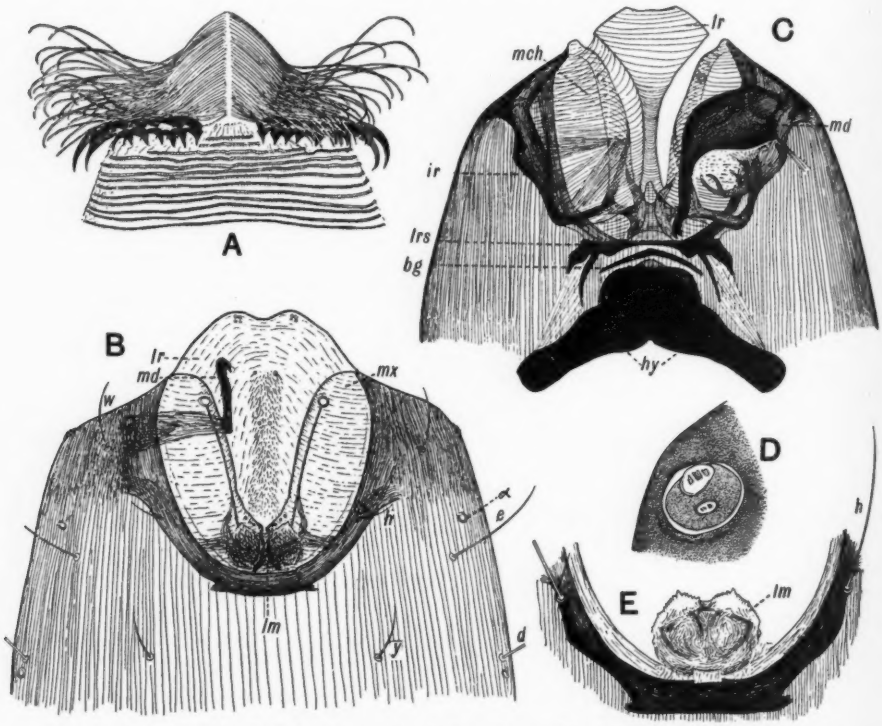


Fig. 2. *Apelma bromelicola* Lutz. Larva: **A**, prothoracic pseudopod. **B**, ventral view of mouth-parts, with right mandible protruding. **C**, dorsal view of mouth-parts with top of head removed; mandibular chamber of left side intact but mandible removed; right mandible present, retracted, and dorsal wall of chamber removed. **D**, left antenna, highly magnified. **E**, ventral view of lower (posterior) margin of mouth aperture magnified to show labial plate. *Lettering: bg* = bridge of hypopharynx; *ir* = internal rod; *lm* = labium; *lr* = labrum; *lrs* = lateral rod system of hypopharynx; *mch* = mandibular chamber; *md* = mandible; *mx* = maxilla.

portion to protrude between the labrum and the maxillae, in which space it moves freely in the sagittal plane, actuated by the rotation of the basal part. Fungus spores and vegetable detritus of all kinds may thus be carried into the mouth as by a pair of paddles. The mandibles are also employed to some extent during slow progression.

The Maxillae (Fig. 2, B, *mx*, C) are membranous bodies, thin and transparent, projecting from the chitin surrounding the mouth-aperture, their free

edges touching the labrum except when that organ is retracted to permit access to the mouth. The maxillae thus form the floor of the mandibular chamber previously described. Posteriorly the two maxillae meet above the labial plate, where several minute sensory organs are born. The largest sensorium is a circular body on the inner surface near the anterior end, from which a row of very short delicate setae extends to the posterior end.

Labium (Fig. 2, B, E, *lm*): at first sight there appears to be no labial plate present, but if all the other mouth-parts are successfully removed a small bilobed plate with toothed extremity remains. It consists of thin colourless chitin, joined to the posterior margin of the mouth-aperture by still thinner membranous chitin; the whole is very different from the strong projecting plate of *Forcipomyia* s.str. On the other hand, the external labial plate is completely absent in *Thyridomyia* and other allied groups to be described shortly.

In addition to the mouth-parts already described there is a pair of strong inner rods which arise from the anterior converging walls of the head (Fig. 2, C, *ir*); they proceed directly towards the hypopharynx and then bend inwards and downwards to terminate above the labial plate. A branch given off just before the end passes into and merges with the maxilla. The chitinous plates forming the roof of the mandibular chamber join this rod laterally, which thus limits the chamber at the sides and back.

The Hypopharynx (Fig. 2, C, *hy*) is essentially the same complicated structure as found in other Ceratopogonines (Saunders, 1924 *a*). The lateral rod system is slightly different, with its anterior part nearly upright instead of sloping back sharply. The main body of the hypopharynx consists as usual of a middle dorsal sclerite with two lateral wings connected by suspensory rods to the ventral sclerite, which receives the salivary duct at its anterior margin. The bridge is present unmodified, in front of the dorsal sclerite (*bg*).

Body. The body is composed of the usual three thoracic and eight abdominal segments (Fig. 4, C), the eighth being divided into two apparent segments; all are compressed dorso-ventrally. The prothorax bears a ventral pseudopod, and the last abdominal segment a sub-anal hook-studded ridge.

The Prothoracic Pseudopod (Fig. 2, A) is different from that of any other Ceratopogonine larva at present known. It consists of an undivided fleshy protrusion of the anterior wall of the ventral surface of the prothorax, directed forwards and downwards. It bears two rows of golden-brown thorn-like hooks on either side of the median line, comprising 6 and 8 respectively, and beyond these, on the conical apex, a great number of very slender, curving, hair-like hooks laterally directed. The broad base of the pseudopod is marked on its posterior surface with many transverse ridges bearing minute hooks. The combination of strong hooks and hair-like ones in such quantities is unique among Chironomid larvae.

The Posterior Pseudopod consists of a row of five thorn-like hooks on either side of the median line, and a second row of four pale slender ones, all directed

forwards; this is the number and arrangement found in nearly all *Forcipomyia* and *Atrichopogon* larvae. These hooks come into use when the larva wishes to move fast, the procedure being interesting and unusual owing to the confined space in which it lives. The posterior end of the body is bent to one side until the extremity of the body is about on a line with the middle of the body; the larva then grips the substratum with its posterior pseudopod and straightens itself, thrusting the body forward, while the extremity of the abdomen makes a half turn, pivoting upon its temporary point of attachment. *Orphnephila* and *Dixa* larvae move in the horizontal plane, but their body is bent quite differently (Thienemann, 1909); *Forcipomyia* larvae on a wet surface tend to move somewhat after this fashion, but sluggishly and to no set purpose.

The Anal Blood-gills: some variation occurs in these organs among different species. They may be similar to those of *Forcipomyia* s.str. in which case each of the two gills is bilobed, or they may resemble more nearly those of *Culicoides*, each lobe being subdivided so that there are in all eight delicate pointed processes protruding from the anus (Fig. 1, C, *ag*).

The Cauda: this term is here introduced to designate the median posterior prolongation of the body above the anus. It is strikingly analogous to the cauda of aphids, and the term is also used in much the same sense in describing Elaterid larvae. In *Apelma* larvae the cauda is short and bluntly conical (Fig. 1, C, *ca*); in other genera it is long and very characteristic, so that a suitable term has become a necessity.

Chaetotaxy: the chaetotaxy is most distinctive for the group, but is practically identical in all species, and is therefore of little use for specific determination. Long slender macrochaetae are arranged along the sides of the body (Fig. 4, C), one pair on the prothorax, two pairs each on the meso- and metathorax, three pairs each on the first seven abdominal segments, and one pair on the first half of the eighth. In some species these are "finned" (Fig. 1, D). On the dorsum of the mesothorax there is a long pair, always simple, and a shorter pair on the metathorax; on the posterior margin of the first half of the eighth abdominal segment there is a long pair of simple macrochaetae arising from a common or double chitinous tubercle. At the extremity of the body there is a dorsal and a lateral pair of short blade-like modified hairs (Fig. 1, C, E). Of microchaetae there is a dorsal pair on each of the first seven abdominal segments, possibly homologous with the *a* hairs of *Forcipomyia* and *Atrichopogon* larvae; between these and the lateral chaetae there are three microchaetae on either side. On the prothorax there are two ventrolateral pairs of longer microchaetae. The latero-ventral thoracic groups representing the sensory organs of the legs consist of two long and two short microchaetae (Fig. 1, F).

The Malpighian Tubules are three in number in those species (*edwardsi* and *bromelicola*) of which sufficient material is available to permit dissection.

Pupa.

The most important character of the pupa is the ventral position of the male sexual processes of the last abdominal segment, which separates the group from *Forcipomyia* and its subgenera, and connects it with *Thyridomyia* and *Atrichopogon*. The posterior median point of the thorax extends only to the anterior border of the first abdominal segment (Fig. 1, I, *pp*) as in the pupae of *Dasyhelea*, *Culicoides*, and most species of *Atrichopogon*, never reaching across the segment as in *Forcipomyia*. On the head two or three papillae occur, either on the median triangle or on the lateral pieces, but never setae. On the thorax there are usually minute tubercles, pits, or microchaetae. On the abdomen the setigerous tubercles on all sides of the segment are suggestive of other aquatic Ceratopogonines (*Bezzia*, *Palpomyia*, etc.), and in one species, *magna*, there are dorsal markings in the cuticle (Fig. 6, D), a condition never yet found in terrestrial forms. Since the larval skin is not retained by the pupa the last abdominal segments bear the same armature as the others, though somewhat modified on the penultimate. The paired processes of the last abdominal segment in both sexes are moderate in length and each bears a short lateral seta.

The Prothoracic Horns are sub-cylindrical, tapered at the base, and sometimes slightly swollen near the tip. The basal two-thirds is imbricated. The spiracular papillae occur distally in a U-shaped loop, which may be open posteriorly or anteriorly. The horns are articulated with the thorax, another connecting link with the aquatic Ceratopogonines, and are usually directed forwards and upwards so that the pupa may float at the surface of the water with its respiratory horns penetrating the surface film.

Adults.

Adults were reared from the early stages of four out of the five species obtained. One proved to be the species described by Lutz (1914) under the name of *Ceratopogon bromelicola*, as was determined by comparison of co-types kindly lent by Dr Lutz himself. A further description of this species is necessary, as the original diagnosis does not furnish sufficient detail to discriminate between the very close species now known. Names for two others have been chosen in honour of prominent workers in Dipterology.

A careful study of the many species of terrestrial Ceratopogonines collected in Brazil and in England has shown that the larvae and pupae point the way to a sound classification of this very confused group. One dependable character has been discovered in the adults to correspond with the larval classification, namely the nature of the internal chitinisations of the male hypopygium; almost all other characters used by specialists of the group are of specific value only. The impossibility of examining the hypopygium without making a special preparation is responsible for its omission from descriptions until a very recent date.

In *Apelma* the internal chitinisations consist of a pair of apodemes from the antero-dorsal rim of the side-pieces passing straight forward into the ninth segment (Fig. 3, L, *ap*). A pair of free spoon-like processes (*pa*) passes backwards from the base of these apodemes, joined together by a strong transverse bar (*tb*); these may be regarded as true parameres since they arise from the end of the genital tube. The apodemes, parameres, and transverse bar form a characteristic H-shaped structure. The term *aedeagus* has been proposed by Sharp, and adopted by Edwards in his study of the homology of the parts of the male hypopygium in Nematocera (Edwards, 1920) for all the chitinous structures of the genital tube, but in the present instance it is advisable to follow the precedent set by Carter, Ingram, and Macfie and reserve the term for the ventral chitinisations only, rather than to cause confusion by introducing a new name.

The one other outstanding character of the adults of the genus is the absence of empodia between the claws of the males.

Specific Descriptions.

Apelma edwardsi n.sp.

Larva. General appearance of body colourless, matching perfectly the white inner surface of the leaves of the host plant. *Head* dark brown to black; proportion of width to length, 10 : 16·3; greatly flattened (Fig. 1, B). Macrochaetae of *body* light brown, inconspicuous; lateral chaetae with basal fin-like expansions (Fig. 1, D). *Anal blood-gills* each 4-lobed (Fig. 1, C, *ag*). *Length* about 4·5 mm.

Pupa. (Fig. 1, I). Colour (exuvia) ochreous throughout in specimens from Pernambuco, dorsum of thorax fuscous in Rio examples. *Head* with three papillae on median triangle. *Thorax* with two pairs of setigerous papillae and two pairs of pits. *Abdomen:* each segment with three pairs of minute dorsal papillae, the anterior pair setigerous (setae much longer in Rio specimens than in Pernambuco examples); a double lateral tubercle, the anterior part bearing a long seta, the posterior a short spine; three pairs of ventro-lateral tubercles with short spines; one pair of ventral microchaetae. *Prothoracic horns* (Fig. 1, G) with slight swelling on posterior surface above middle; spiracular papillae about 12 on distal extremity in incomplete ellipse open on inner side (Fig. 1, H). *Length* 2·3–2·8 mm.

Adult: Female. *Eyes* bare, black, contiguous. *Occiput* grey, with many large black hairs and yellowish pubescence. Membranes of face ochreous. *Fronto-clypeus* and *proboscis* strongly ochreous. *Antennae* (Fig. 3, A) dark, with black hairs; first three segments of flagellum transverse, without neck, next five becoming gradually more spherical; change from eighth to ninth flagellar segment very pronounced; proportion of first eight segments to last five, 26 : 48; last five, 7 : 8 : 10 : 10 : 13; ultimate segment $4\frac{1}{2}$ times as long as wide including knobbed stylet, which is asymmetrical (Fig. 3, C). *Palps* (Fig. 3, N) pale, with grey markings on segments 3, 4, 5. First segment greatly

reduced; third swollen in proximal two-thirds, bearing a sunken chitinous sensory cylinder; distal portion of third reduced to a narrow neck, pale; all segments pubescent, bearing a number of slender chaetae, longer on proximal segments than on distal; proportional length of segments, 10 : 20 : 32 : 18 : 17. *Thorax* grey on dorsum, clothed with golden pubescence and longer black hairs; humeral angles and pleurae pale ochreous, venter slightly fuscous.

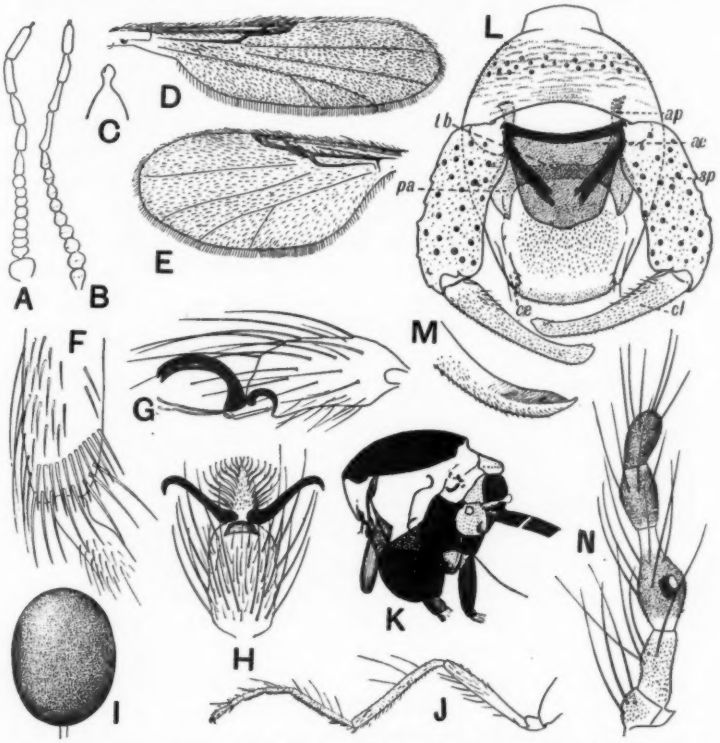


Fig. 3. *Apelma edwardsi* n.sp., adult characters. **A**, female antenna. **B**, male antenna. **C**, tip of last antennal segment. **D**, male wing. **E**, female wing. **F**, tip of tibia of first pair of legs. **G**, lateral view of last tarsal segment and claws of male. **H**, dorsal view of last tarsal segment of female. **I**, spermatheca of female. **J**, hind leg of male. **K**, lateral view of thorax of male. **L**, ventral view of hypopygium of male. **M**, tip of clasper, highly magnified. **N**, left palp of female. *Lettering:* *ae* = aedeagus; *ap* = apodeme of side-piece; *ce* = cerci; *cl* = clasper of forceps; *pa* = paramere; *sp* = side-piece of forceps; *tb* = transverse bar.

Scutellum pale, postscutellum black. *Halteres:* stem greyish, knob pale yellow. *Wings* (Fig. 3, E) iridescent, clothed with short dark decumbent macrotrichia, fringe long. Costa ending at about middle of wing; first radial cell almost obliterated by fusion of veins, second distinct after staining, narrow; cubitus forking just before middle of wing. *Legs* ochreous, slightly fuscous on tarsi; clothed with fine golden hairs and long black ones; two comb-like rows of

chaetae occur on the inner surface of the extremity of all tibiae, most noticeable on first (Fig. 3, F); a small apical spine on tibiae, none on femora. First segment of hind tarsus about as long as next three together; proportional length of segments, 29 : 9 : 8 : 6 : 6. Claws simple; empodium well-developed, bearing long, curved, spatulate hairs, many with a small branch hair near tip (Fig. 3, H). *Abdomen:* tergites and sternites black, with many black hairs; pleural membrane pale, pubescent. Cerci pale. *Spermathecae* 53 × 41 μ, two, subspherical, well-chitinised, duct unchitinised (Fig. 3, I). *Length*[1] 1·65 mm. *Wing* 1·0 × 0·8 mm. *Antenna* 0·6 mm.

Male. *Eyes* bare, black, contiguous. *Occiput* grey-green, with golden pubescence and many large black hairs. *Face* and *proboscis* pale, as in female. *Antennae* (Fig. 3, B) dark, almost black, with long hairs black, pubescence of distal segments white. Segments 2, 3, 4 of flagellum practically without neck, transverse, subsequent segments becoming gradually narrower. Proportion of first eight flagellar segments to last five, 38 : 47; last five, 5 : 12 : 10 : 9 : 11; ultimate segment 3½ times as long as wide, including terminal asymmetrical knobbed stylet. *Palps* as in female, but segment 3 less swollen; proportional length of segments, 8 : 25 : 32 : 14 : 15. *Thorax* uniformly grey-green on dorsum in dried specimens, black when in spirit, with large black chaetae and golden pubescence; humeral angles pale; scutellum pale, postscutellum black. Pleural and ventral sclerites pigmented as in Fig. 3, K. *Halteres:* stem yellowish dusky, knob white. *Wings* (Fig. 3, D) iridescent, with pale golden surface and fringe hairs, and dark macrotrichia on anterior veins. Costa reaching beyond middle of wing; first radial cell almost obliterated, second distinct; cubitus forking beneath extremity of costa. *Legs* (Fig. 3, J) pale ochreous, fuscous on tarsi; large hairs black, pubescence pale yellow; double comb-like row of chaetae and spur on extremity of tibiae as in females. First segment of hind tarsi as long as next three together; proportional length of segments, 21 : 8 : 7 : 5 : 6. Claws large, slender, with slightly bifid ends; empodium replaced by a pair of long spatulate hairs (Fig. 3, G). *Abdomen:* tergites and sternites black, with black hairs; pigmentation of first sternite a transverse bar with extremities bent forwards; second divided into two widely separated longitudinal bars; third to sixth indistinctly divided by hyaline area; seventh and eighth, undivided transverse bars. *Hypopygium* (Fig. 3, L): anterior neck of ninth tergite with even margin, unchitinised. Membranous anal portion (tenth segment) projecting slightly beyond ninth tergite; lateral fleshy claspers or cerci (*ce*) small, with four short chaetae. Aedeagus (*ae*) well-chitinised, subrectangular or shield-shaped, posterior margin somewhat prolonged in middle. Parameres (*pa*) terminating in short spoon-like plates, poorly chitinised; joined by strong cross-bar (*tb*), forming with the apodemes of the side-pieces (*ap*) an H-shaped internal structure. Side-pieces of forceps (*sp*) cylindrical, slightly narrower in middle, not tapering; bearing many long chaetae. Claspers equal

[1] All adults are measured from the anterior margin of the thorax to the tip of the abdomen when normally distended by fixation in Carnoy, or when softened in carbolic acid after drying.

in length to side-pieces, slender, tapering, with slightly swollen, grooved or hollowed tips. *Length* 1·8 mm. *Wing* 1·2 × 0·3 mm. *Antenna* 0·7 mm. Described from numerous larvae and pupae, 9 females, and 4 males, dry and in spirit, from small Bromeliads on rocks in Rio Bay and on Island of Paquetá, Brazil, 23. viii. 23; also the predominating species in terrestrial Bromeliads in woods behind Pernambuco (Dois Irmãos), Brazil, 10. ix. 23. Types deposited in British Museum.

Apelma bromelicola Lutz 1914.

Larva. General appearance pale yellowish, stronger orange-yellow on thorax. *Head* ochreous, eyes and hypopharynx showing through black; proportion of width to length, 10 : 11·4 (Fig. 4, A). Macrochaetae of *body* all simple, inconspicuous. *Anal blood-gills* each bilobed. *Length* about 4·0 mm.

Pupa (Fig. 4, D). Colour (exuvia) ochreous, thorax fuscous. *Head* with two pronounced papillae on median triangle. *Thorax* with two pairs of minute tubercles and a pair of microchaetae on dorsum. *Abdomen:* each segment with the usual double lateral tubercles, three pairs of ventro-lateral tubercles with short spines, three pairs of dorsal microchaetae, and one ventral pair (Fig. 4, F). *Prothoracic horns* (Fig. 4, E) sub-cylindrical, swollen very slightly at two-thirds their length; imbrications slight, even; spiracular papillae about 14 in a **U**-shaped loop opening posteriorly. *Length* 2·3 mm.

Adult: Female. *Occiput* dark, with large black hairs and golden pubescence. *Fronto-clypeus* and *proboscis* light ochreous. *Antennae* dark brown; basal segments of flagellum strongly compressed, transverse, becoming subspherical at fifth; ninth flagellar segment twice the length of eighth; proportion of first eight to last five, 19 : 34; last five, 7 : 5 : 6 : 6 : 10; ultimate segment stout, with slender terminal stylet. *Palps* dark. Third segment much shorter than in *edwardsi*, though of same width (23 units long); other segments collapsed and twisted in only available specimen. *Thorax* dark greyish brown on dorsum, including humeral angles; pleurae pale, with faint markings on sclerites. Scutellum and postscutellum dark brown to black. *Legs* ochreous, with last segments of tarsi fuscous; clothed with long black hairs and golden pubescence; proportional length of hind tarsal segments, 30 : 10 : 9 : 6 : 6. *Wings* clothed rather sparingly with dark macrotrichia; costa terminating at about middle of wing; first radial cell almost obliterated, second distinct; cubitus forking well before middle of wing. *Halteres* with pale knob and slightly fuscous stem. *Abdomen:* tergites and sternites grey; pleural membrane pale, pubescent. Cerci pale. *Spermathecae* two, about 55 × 40 μ, elliptical, dark, duct unchitinised. *Length* about 1·4 mm. *Wing* 0·9 × 0·35 mm. *Antenna* 0·45 mm.

Male. *Face, fronto-clypeus, proboscis* dark brown to black, with narrow pale line around base of antennae. *Antennae:* torus dark brown to black, flagellum light brown; basal segments of flagellum transverse, remainder up to ninth globular; distal segments deeply sculptured; proportion of first eight to last

five flagellar segments, 35 : 44; last five, 6 : 11 : 9 : 8 : 10; last segment three times as long as wide, including terminal simple knobbed stylet. *Palps* brown. Third segment slightly swollen in middle, tapering equally at each end (Fig. 4, I); sensorium at middle of segment; proportional lengths, 8 : 15 : 27 : 13 : 11. *Thorax* uniform dull brown on dorsum, including humeral angles; pubescence golden. Pigmentation of pleural sclerites as in Fig. 4, G. Scutellum and post-

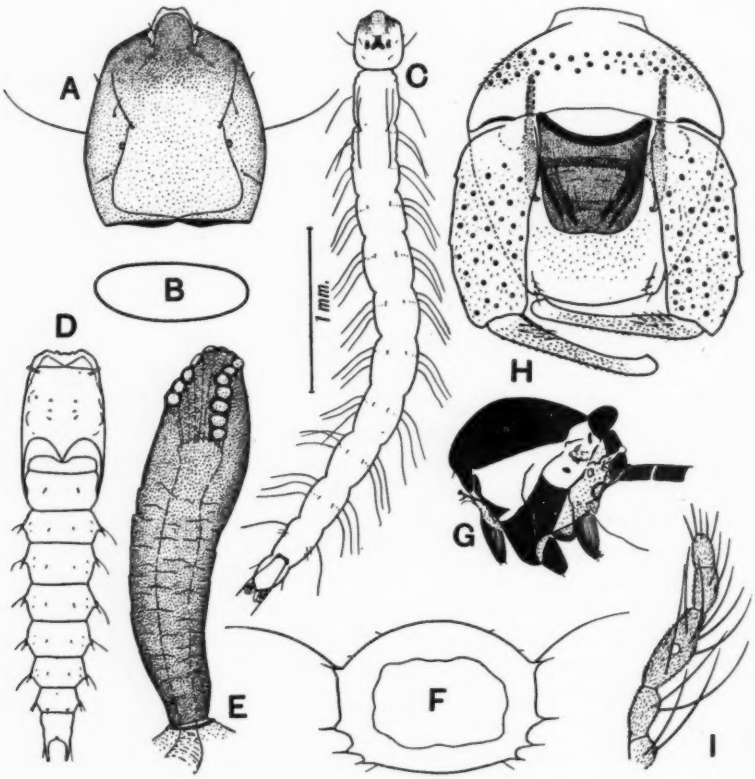


Fig. 4. *Apelma bromelicola* Lutz. Larva: **A**, dorsal view of head. **B**, cross section of head. **C**, dorsal view of entire larva. Pupa: **D**, entire pupa. **E**, posterior view of left prothoracic horn. **F**, posterior view of single abdominal segment. Adult: **G**, lateral view of male thorax. **H**, ventral view of male hypopygium. **I**, right palp of male.

scutellum dark brown to black. *Legs* strong ochreous, fuscous on tarsi; tibiae without definite double comb-like row of chaetae at distal extremity; proportional length of hind tarsal segments, 22 : 9 : 8 : 6 : 6. *Wings* thinly clothed with pale macrotrichia. First radial cell practically obliterated, second short; costa terminating at about middle of wing; cubitus forking beyond end of costa. *Halteres* pale, with slightly fuscous stem. *Abdomen:* tergites and

sternites dark, first sternite crescentic. *Hypopygium* (Fig. 4, H) anterior neck of ninth tergite short, with even margin, poorly chitinised. Aedeagus well-chitinised, sub-rectangular, the posterior border slightly indented in middle, not prolonged as in other species. Claspers of forceps with characteristic swollen tips. *Length* 1·62 mm. *Wing* 1·2 × 0·3 mm. *Antenna* 0·65 mm.

Described from many larvae, 2 pupae, and 1 male in spirit, from small Bromeliads on rocks in Rio Bay, 23. viii. 23; also 2 males pinned and 1 female in canada balsam, lent by Dr A. Lutz, reared from Bromeliads on Governor's Island, Rio, no date. Specimens deposited in British Museum.

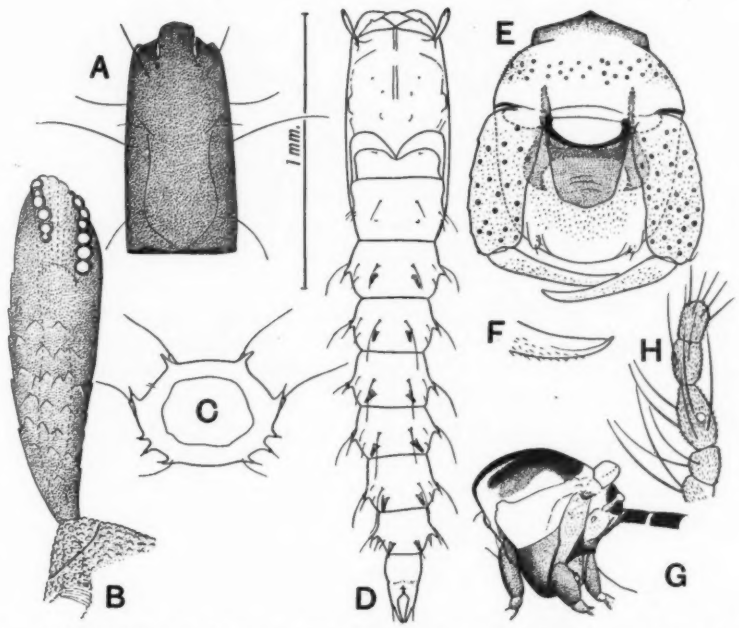


Fig. 5. *Apelma keilini* n.sp. Larva: **A**, head. Pupa: **B**, posterior view of left prothoracic horn. **C**, posterior view of single abdominal segment. **D**, pupa, entire. Adult: **E**, ventral view of male hypopygium. **F**, tip of clasper. **G**, lateral view of thorax of male. **H**, left palp of male.

Apelma keilini n.sp.

Larva. In general appearance similar to *edwardsi*, but head light brown instead of black. Macrochaetae simple, inconspicuous. *Head* very long and narrow (Fig. 5, A), proportion of width to length, 10 : 20·8. *Anal blood-gills* each 4-lobed, as in *edwardsi*. *Length* about 4·0 mm.

Pupa (Fig. 5, D). Colour (exuvia) ochreous throughout. *Head* with a papilla on each lateral piece, none on median triangle. *Thorax* with two pairs of sensory pits and one pair of large low tubercles. *Abdomen:* each segment with one pair of tubercles with long setae, one pair of cuticular spines, and

two pairs of microchaetae on dorsum, in addition to normal lateral and latero-ventral setigerous tubercles (Fig. 5, C). *Prothoracic horns* (Fig. 5, B) sub-cylindrical, not swollen; imbrications coarse, pointed; spiracular papillae about 15, in U-formation opening posteriorly. *Length* 2·2 mm.

Adult: Male. *Occiput* light brown. *Fronto-clypeus* and *proboscis* pale ochreous. *Antennae:* torus ochreous with fuscous rim; flagellum pale. Form of flagellar segments much as in other species; proportion of first eight to last five flagellar segments, 30 : 45; last five, 3 : 10 : 11 : 10 : 11; ultimate segment $3\frac{1}{2}$ times as long as wide, including terminal simple knobbed stylet. *Palps* pale, short (Fig. 5, H). Segment 2 comparatively much shorter than in *edwardsi*, *bromelicola*, or *magna*; segment 3 stout, slightly tapered distally; proportional length of segments, 7 : 10 : 20 : 13 : 12. *Thorax* grey to black on dorsum, pigmentation not extending down as far as lateral suture of notum; humeral angles pale, the area extending backwards in a streak on either side of the median band (Fig. 5, G). Venter grey, extending up pleurae very slightly. Scutellum pale, postscutellum black. *Legs* pale ochreous, slightly fuscous on tarsi; tibiae without distinct apical comb-like double row of chaetae; proportional length of hind tarsal segments, 15 : 6 : 5 : 5 : 5. *Wings* not appreciably different from those of other species. *Halteres:* stem and knob pale. *Abdomen:* tergites and sternites black; first sternite a straight, narrow, transverse bar. *Hypopygium* (Fig. 5, E): anterior neck of ninth sternite pointed in middle, moderately chitinised. Aedeagus shield-shaped with transverse creases. Posterior spoon-like extremities of parameres expanded, distinct. Claspers of forceps tapering; extremity hollowed, not swollen, with thin inward-turned tip. *Length* 1·55 mm. *Wing* 0·9 × 0·35 mm. *Antenna* 0·8 mm.

Described from 3 larvae, 3 pupae, and 1 male in spirit, from terrestrial Bromeliads in woods behind Pernambuco (Dois Irmãos), Brazil, 10. ix. 23. Types deposited in British Museum.

Apelma magna n.sp.

Larva. General appearance so similar to *edwardsi* that the larvae could not be distinguished macroscopically; obtained by rearing larvae associating with characteristic pupae in certain Bromeliad plants. (No pupae of *edwardsi* were obtained from these plants.) Larvae somewhat larger than *edwardsi*, colouring the same, macrochaetae of sides "finned." *Head* dark brown to black, proportion of width to length, 10 : 16·2 (Fig. 6, A). *Anal blood-gills* each subdivided as in *edwardsi*. *Length* about 5·2 mm.

Pupa (Fig. 6, D). Colour (exuvia) strongly fuscous in all parts except sides and venter of thorax, which are pale ochreous; cuticular markings occur on dorsum of abdominal segments. *Head* with two papillae on median triangle. *Thorax* with two pairs of minute papillae and a pair of pits on dorsum. *Abdomen:* each segment with one dorsal pair of microchaetae and three pairs of minute papillae in addition to the normal setigerous tubercles. *Prothoracic horns* (Fig. 6, B) swollen before tip; imbrications not pronounced; spiracular

papillae about 14 in loop opening anteriorly (Fig. 6, c), more like *edwardsi* than other species. *Length* 3·5 mm.

Adult. The species differs from *edwardsi* chiefly in size and in the colour of the pupae. The following are the differential chracters which may be found in the adults:

Female. Colour somewhat paler, abdominal sternites scarcely pigmented at all. *Antennae* and *palps* more distinctly pubescent; proportional length of

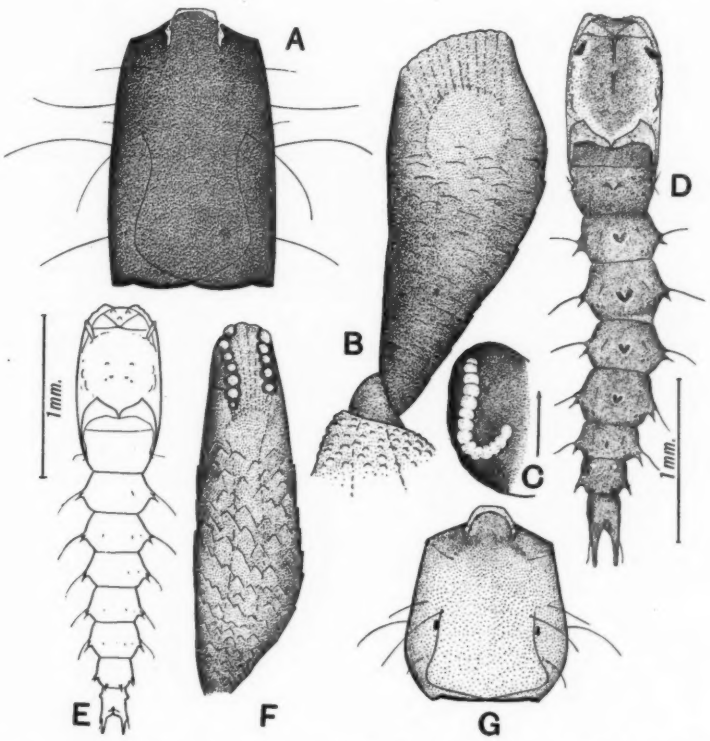


Fig. 6. *Apelma magna* n.sp. Larva: **A**, head. Pupa: **B**, outer view of left prothoracic horn. **C**, top of left prothoracic horn. **D**, pupa, entire.
Apelma sp. Pupa: **E**, entire pupa. **F**, posterior view of right prothoracic horn. Larva: **G**, head.

segments the same. *Spermathecae* two, 83 × 76 μ, nearly spherical, dark, duct unchitinised. *Length* 1·9 mm. *Wing* 1·24 × 0·38 mm. *Antenna* 0·9 mm.

Male. Tip of claspers of forceps not swollen, a simple blunt point, not hollowed as in *edwardsi*. *Length* 2·15 mm. *Wing* 1·24 × 0·33 mm.

Described from 4 larvae, 4 pupae, 2 males and 1 female in spirit, from terrestrial Bromeliads in woods behind Pernambuco (Dois Irmãos), Brazil, Sept. 1923. Types deposited in British Museum.

Apelma sp.

Larvae and pupae of another species besides those already described were taken, but adults failed to emerge. The characters of the early stages are given, however, to add to our knowledge of the genus.

Larva. In general appearance similar to *bromelicola*, but rather stouter; brighter orange-yellow all over. Macrochaetae simple, black, conspicuous. *Head* pale yellowish, hyaline, showing eyes and hypopharynx distinctly; proportion of width to length, 10 : 12·5 (Fig. 6, G). *Anal blood-gills* each bilobed. *Length* about 3·8 mm.

Pupa (Fig. 6. E). Colour (exuvia) ochreous throughout. *Head* with three papillae on median triangle. *Thorax* with two pairs of papillae and one pair of pits. *Abdomen:* each segment with two pairs of dorsal microchaetae, no papillae; larger setigerous tubercles normal. *Prothoracic horns* (Fig. 6, F) swollen on inner surface before middle, with many pointed imbrications; spiracular papillae about 14 in **U**-shaped loop opening posteriorly. *Length* 2·7 mm.

Described from 2 larvae and 4 pupae, taken sparingly among other species in terrestrial Bromeliads in woods behind Pernambuco (Dois Irmãos), Brazil, 10. ix. 23.

GENUS **THYRIDOMYIA** N.G.

Larvae with rudimentary antennae devoid of a flagellar segment; prothoracic pseudopod undivided, with many rows of minute hooks; cauda absent.

Pupae with male sexual processes ventral; abdominal segments with papillae on all surfaces.

Adults with macrotrichia on wings; first tarsal segment as long as next three together; empodia well-developed. Females with basal flagellar segments of antennae compressed, transverse. Males with ninth sternite as long as its greatest width, bearing a membranous "window[1]" of varying size; internal chitinisations of hypopygium in form of apodemes from side-pieces passing straight forwards, produced in the frontal plane into triangular plates which may or may not join each other medially.

These are in brief the characters which separate the genus from the allied genera *Apelma, Forcipomyia* and *Atrichopogon*. Since the early stages are known only in one species it is impossible to foretell which of the other distinguishing larval characters will be constant throughout the genus, but those given above are almost certainly reliable, and should serve to identify new species without difficulty.

Students of the Ceratopogonines will recognise that the long first tarsal segment of the adults should place this group in Malloch's genus *Euforcipomyia* (1915). Unfortunately, the character in question (the chief means of distinguishing the genus) is exhibited by *Apelma* and several distinct sub-

[1] Hence the generic name, θύρις, -ίδος, a window or small door, and μυῖα, a fly.

genera of *Forcipomyia* (to be published shortly); in fact it is the long second tarsal segment of *Forcipomyia* s.str. that is exceptional among Ceratopogonines, and even there it is not constant. Malloch's type, *hirtipennis*, has the basal nine flagellar segments of the female antennae "distinctly but not greatly longer than broad" which does not, therefore, fit the group under discussion. In the writer's opinion the name *Euforcipomyia* cannot be used until the male of the type species has been described, since the clue to the natural grouping of these terrestrial Ceratopogonines, apart from the early stages, lies in the internal chitinisations of the male hypopygium.

The type of the genus is *Thyridomyia palustris* n.sp., all stages of which are here described and figured in detail.

Thyridomyia palustris n.sp.

Larva.

Very small, about 2·6 mm. when full-grown. *Colour* strong orange; peripheral fat-body yellowish, with gut, plasma, and perivisceral fat-body showing through orange red. Head dusky orange, black around mouth.

Head. The head is comparatively small in full-grown larvae, and is shorter and deeper than in any group of *Forcipomyia* (Fig. 7, A, I). The head capsule bears a number of large protuberances situated as follows: an admedian pair on the vertex with conical apex projecting forwards; a smaller, lower conical pair lateral to these; a vague, indefinite raised area still further to the sides; a lateral pair slightly further forwards with rectangular rather than conical form; and a median confluent pair of varying size nearly half-way down the front of the head. The presence of such protuberances constitutes a radical difference from any *Forcipomyia* larvae, but approaches the condition found in the head of some *Atrichopogon* species, and also is strikingly analogous to the head of *Orphnephila* larvae (Saunders, 1923). In addition to these the *eye* protrudes to a marked extent.

The Antennae are most unusual in having the normal basal portion but not the flagellar segment found in *Forcipomyia* and *Atrichopogon*. Furthermore, the organ has migrated down the head almost to the *t* hairs, the eye accompanying it. In place of a flagellum the basal portion contains in its orifice an extrusible ring-like band of chitin, with two minute, ill-defined, sensory processes in the surrounding membrane on the outer side (Fig. 7, E). We have here evidence of relationship with *Apelma*, in which genus the antennae have moved all the way down the head, and are still more reduced (Fig. 1, A, *an*; 2, D).

The Mouth-parts are of the normal *Forcipomyia* and *Atrichopogon* type, and lack an external labial plate. The mandibles are straight, and terminate in two pronounced lobes (Fig. 7, F). On the top of the labrum there is a pair of small capitate sensory processes, slightly fuscous; a similar process occurs on each maxilla below the normal cylindrical sensorium.

Chaetotaxy (Fig. 7, I): the normal hairs *p* and *q* of the *Forcipomyia* head are readily recognisable in *Thyridomyia* though somewhat displaced; each is situ-

ated on a large papilla, which in the case of the *q* hairs is long and cylindrical. The other hairs and pits may be homologised with those of *Atrichopogon*; there

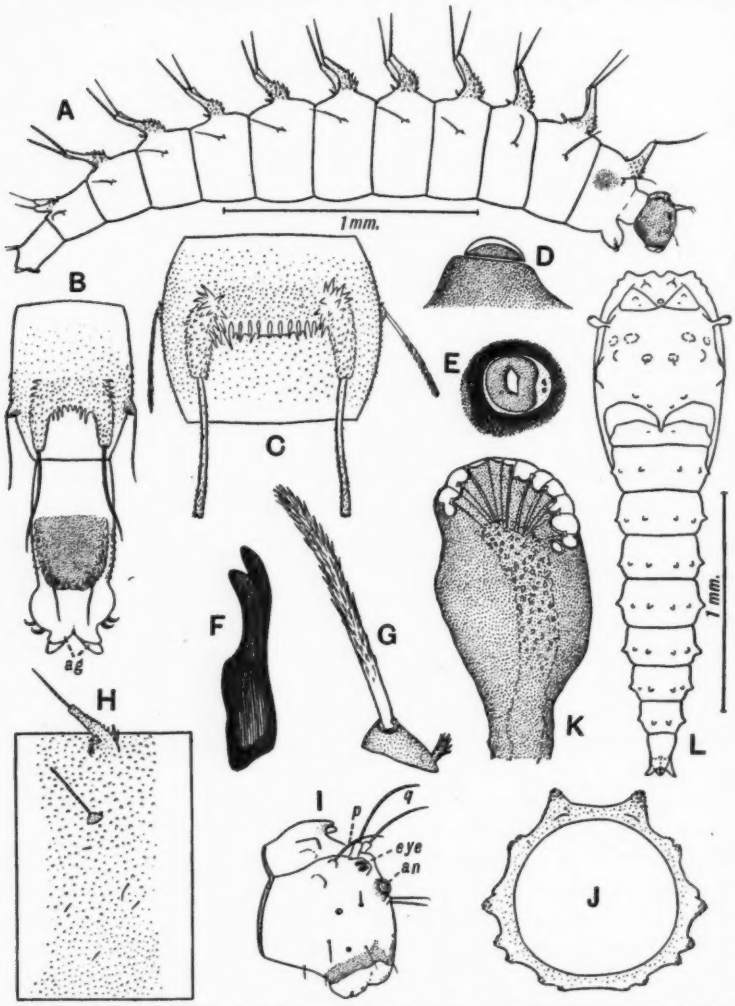


Fig. 7. *Thyridomyia palustris* n.sp. Larva: **A**, lateral view of entire larva. **B**, dorsal view of extremity of abdomen. **C**, dorsal view of 3rd abdominal segment. **D**, lateral view of antenna. **E**, dorsal view of right antenna. **F**, mandible. **G**, lateral chaetae of body segments, highly magnified. **H**, setal plan of abdominal segment. **I**, lateral veiw of head. Pupa: **J**, posterior view of single abdominal segment. **K**, left prothoracic horn. **L**, pupa, entire. *Lettering: ag* = anal blood-gills; *an* = antenna.

is a very fine hair situated directly upon the lens of the eye, which is obviously homologous with the ocular seta of that genus.

Body. The Prothoracic Pseudopod is rounded, without any indication of median division. The hooks at the apex are in two rows, the anterior consisting of six slender hooks on either side of the median line, and the posterior of four smaller thorn-like hooks similarly grouped.

The Posterior Pseudopod consists of the usual transverse ridge bearing two rows of eight black curved hairs.

The Cauda is completely absent.

The Anal Blood-gills are very short and stout; there are two lobes on either side of the anus (Fig. 7, B, *ag*).

Chaetotaxy: on the dorsum of each segment except the last half of the eighth there is a pair of long tapering outgrowths of the body wall bearing at their tip a seta, the *a* hair; the condition is commonly met with in *Atrichopogon* larvae. These processes are joined together across the dorsum by a stronger deposit of chitin, and along the posterior edge of the plate thus formed there is a row of backward- and upward-directed spines, the central five or six of which are chisel-shaped with serrate extremities (Fig. 7, C). The dorsal processes are themselves very spiny at the base. Of the lateral chaetae found in *Forcipomyia* larvae only one remains of normal size, with a minute many-tipped spine on its basal papilla (Fig. 7, G); the normal hair is possibly *d*, with *b* very greatly reduced but still arising from the same basal papilla, a confluence which often occurs in *Forcipomyia* s.str. All the other hairs are reduced to minute spines, very difficult to discover among the cuticular armature. A thicker deposit of chitin occurs on the sides of the prothorax behind the lateral hair (Fig. 7, A).

The Salivary Glands are comparatively straight and ribbon-like, neither lobed (*Apelma*) nor curved into an **S** (*Forcipomyia*).

Number of *Malpighian Tubules* three.

Pupa.

Colour yellowish orange, darker on thorax. Exuvia ochreous, slightly stronger on thorax. *Head* (Fig. 7, L) with three papillae on the median triangle, the anterior pair setigerous, and a larger and smaller papilla on each of the lateral pieces. *Thorax* with a number of hyaline, slightly raised areas on the dorsum, only the central pair of which are setigerous; other species will probably be discovered in which long spines occur in place of these areas. The median posterior prolongation of the thorax extends for a short distance over the first abdominal segment, a condition reminiscent of *Forcipomyia* but occurring occasionally in *Atrichopogon*. *Abdomen* bearing a number of protuberances all round each segment, the disposition of which is best seen in Fig. 7, J. The larval skin is shed completely at pupation, and the cuticular armature extends unchanged to the eighth segment. The terminal processes on the last segment of both sexes are short, abruptly tapering, and divergent; the male sexual processes are ventral as in *Apelma*, *Atrichopogon*, *Dasyhelea*, and *Culicoides*, whereas in all groups of *Forcipomyia* at present known they are

dorsal. *The Prothoracic Horns* are not very distinctive in this species. They are of dense, rough chitin, of the shape shown in Fig. 7, K, with a row of spiracular papillae round the distal extremity. These are not simple papillae as in *Forcipomyia* s.str. but consist of an upper and a lower palisade as in species of the *ingrami* group (to be described in a future paper), though very closely approximated. *Length* 2·3 mm.

Adults.

Female. *Eyes* narrowly contiguous. *Occiput* large, dark brown to black, clothed with curved brown hairs and fine pubescence. *Vertex*[1] black. Membranes of face creamy white. *Fronto-clypeus* and *proboscis* dark brown. *Palps* (Fig. 8, C) dark brown; third segment greatly swollen, with small distal neck comprising only one-fifth of the length of the segment; sensorium composed of a large number of pedicellate spherical bodies arising from saucer-like depressions, the whole being distinctly outlined only proximally; fourth segment much longer than fifth; proportional length of all segments, 9 : 15 : 28 : 18 : 11. *Antennae* (Fig. 8, E) dark brown throughout; first eight flagellar segments compressed, transverse; last five gradually increasing in length, with only a slight change in length between eighth and ninth; proportion of first eight to last five, 22 : 25; last five, 7 : 9 : 10 : 10 : 14; terminal stylet moderately swollen, faintly notched distally. *Thorax* uniform shining dark brown to black on dorsum, including humeral angles; clothed with pale brown hairs. Pleural sclerites dark brown, membranes creamy white. Scutellum fawn brown, postscutellum dark brown to black. *Legs* strongly fuscous; all segments unarmed; proportional length of hind tarsal segments, 26 : 10 : 9 : 6 : 7. Empodia long, narrow, hairy. *Wings* unadorned, clothed with short, simple macrotrichia scarcely if at all flattened; fringe hairs long, simple; microtrichia distinct. Costa reaching well beyond middle of wing; first radial cell obliterated by fusion of veins, second long, narrow (Fig. 8, B); cubitus forking at middle of wing. *Halteres* with dusky stem, knob chalky white. *Abdomen:* tergites uniform brown; sternites brown, with pigmentation broken to a variable degree; eighth segment a complete ring. Pleural membrane very hairy. Cerci pale, with brown tips. *Spermatheca* 74 × 46 μ, one, pyriform, with narrow end curved to one side; well-chitinised; no chitinisation on duct. *Length* 1·3–1·5 mm. *Wing* 1·0 × 0·45 mm. *Antenna* 0·43 mm.

Male. Coloration of head and proboscis as in female. *Eyes* narrowly contiguous. *Palps* lighter, grey; third segment long and slender, very slightly swollen at two-thirds the length (Fig. 8, F); sensorium a group of pedicellate hairs as in female, but not circumscribed; proportional length of segments, 11 : 18 : 41 : 19 : 14. *Antennae:* torus black, flagellum brown, with macrochaetae black to tip. Proximal segments of flagellum subspherical, gradually becoming elongate; terminal segment stout, with stylet as in female; proportion of first eight segments to last five, 45 : 57; last five, 5 : 23 : 11 : 8 : 10.

[1] The term *vertex* is reserved for that portion of the true vertex which is cut off in the form of a triangle in front of the contiguous eyes.

Thorax with coloration as in female. *Legs* fuscous, all segments unarmed; proportional length of hind tarsal segments, 33 : 14 : 10 : 6 : 6. *Wings* unadorned, clothed more thinly than in female with short macrotrichia; costa ending at middle of wing, first radial cell obliterated, second short and narrow (Fig. 8, A); cubitus forking beyond middle of wing. *Halteres* with dusky stem and chalky white knob. *Abdomen:* tergites uniform brown, with indistinct median line extending to fifth segment; sternites with pigmentation broken into lateral bars and a central marking, on anterior segments, becoming uniform, transverse on seventh segment. Pleural membrane bare, creamy white. *Hypopygium* brown. Ninth sternite as long as its greatest width (in

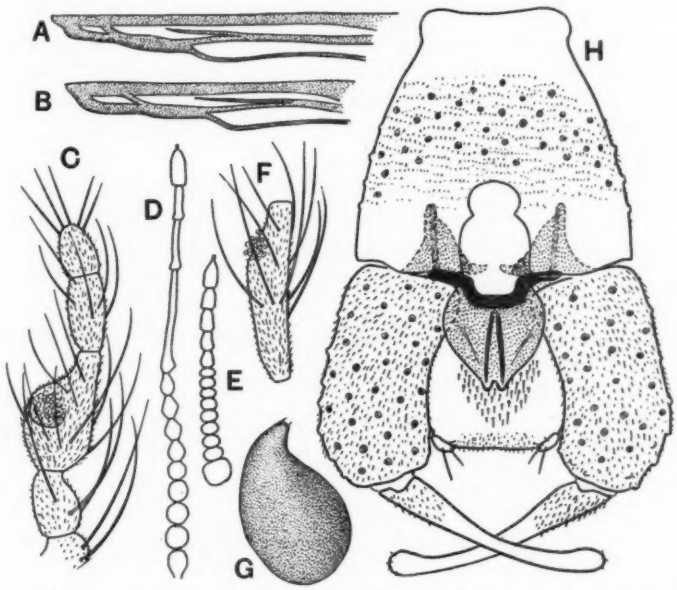


Fig. 8. *Thyridomyia palustris* n.sp. Adult: **A**, anterior wing venation of male. **B**, anterior wing venation of female. **C**, right palp of female. **D**, male antenna. **E**, female antenna. **F**, 3rd segment of palp of male. **G**, spermatheca of female. **H**, ventral view of male hypopygium.

other genera the length varies from less than half to three-quarters the length at most); an unpigmented membranous area occurs on the ventral posterior surface, roughly in the form of a Moorish arch (Fig. 8, H). Aedeagus shield-shaped, with strongly chitinised anterior margin extending into two lateral horns; two ventral carinae run back to the double-pointed posterior extremity. Internal chitinisations in form of triangular plates whose inner angles almost meet in median line; a strengthening rod, the apodeme, passes forward through each plate from the dorsal anterior margin of the side-pieces. Side-pieces curved, cylindrical, slightly broader at extremities; claspers long and slender, with clubbed extremities. *Length* 1·5 mm. *Wing* 1·04 mm. *Antenna* 0·8 mm.

Described from many larvae and pupae, 7 males and 5 females, in spirit, taken in a swampy wood at Little Abington, Cambs., August–December 1924, on rotting moss-grown wood. The species is represented in the British Museum by the following material: 2 ♂, 4 ♀, Corriegills, Arran, 2–4. vi. 1919, swept in bog on shore (F. W. E.); 1 ♂ Quy Fen, Cambs. 17. viii. 21 (F. W. E.); 3 ♂, 8 ♀, Lit. Abington, Cambs. viii. 24 (L. G. S.).

Thyridomyia frutetorum Winn.

Ceratopogon frutetorum Winnertz 1852.
Atrichopogon frutetorum Kieffer 1919.
Forcipomyia aethiopiae Ingram and Macfie 1924.

It is difficult to understand why Kieffer put this species in the genus *Atrichopogon*, since Winnertz' excellent figure of the wing shows that it has not the long second radial cell of that genus. In the same key he includes two other species, *titillans* and *halteratus*, which the writer in a subsequent paper will show to be foreign to *Atrichopogon*.

The original description of *frutetorum* by Winnertz is not sufficiently detailed to discriminate between this species and *palustris*, but through the kindness of Mr F. W. Edwards I have been permitted to examine German specimens in the British Museum identified by Winnertz himself as *frutetorum*. The species is distinct chiefly in the form of the aedeagus of the male hypopygium and in the much larger "window" of the ninth sternite. The female antennae also are markedly different, there being practically no change in length between the eighth and ninth flagellar segments. Figures of the male hypopygium, and the female antenna and palp are given for purposes of identification (Fig. 9, A–D).

The single African male described by Ingram and Macfie (1924 *b*) as *aethiopiae* is practically identical with the specimens of *frutetorum* I have examined. The only substantial difference seems to lie in the partial hairiness of the eyes of the African specimen; this is scarcely sufficient grounds for retaining the species in the face of the identical structures of the male hypopygium. It seems, therefore, that it may be necessary to sink the species, although the great geographical separation is against such a course; future discovery of the early stages and females may justify the re-establishment of the species.

Forcipomyia (?) murina Winn.

Ceratopogon murinus Winnertz 1852.

According to the existing characters of *Forcipomyia* published most recently by Ingram and Macfie (1924 *a*), the common European species *murina* should be included in that genus. In the light of the writer's later investigations there is sufficient evidence to justify the removal of the species from that genus, but not sufficient to place it in any other; at the same time the writer is reluctant to erect a new genus for this one species while ignorant of the early stages. The internal chitinisations of the male hypopygium

(Fig. 9, G) more nearly approach the condition found in *Apelma*, but the species cannot be included in that genus on account of the empodia in the male; the elongated basal flagellar segments of the female antennae also preclude its admission to either *Apelma* or *Thyridomyia*. The species has been

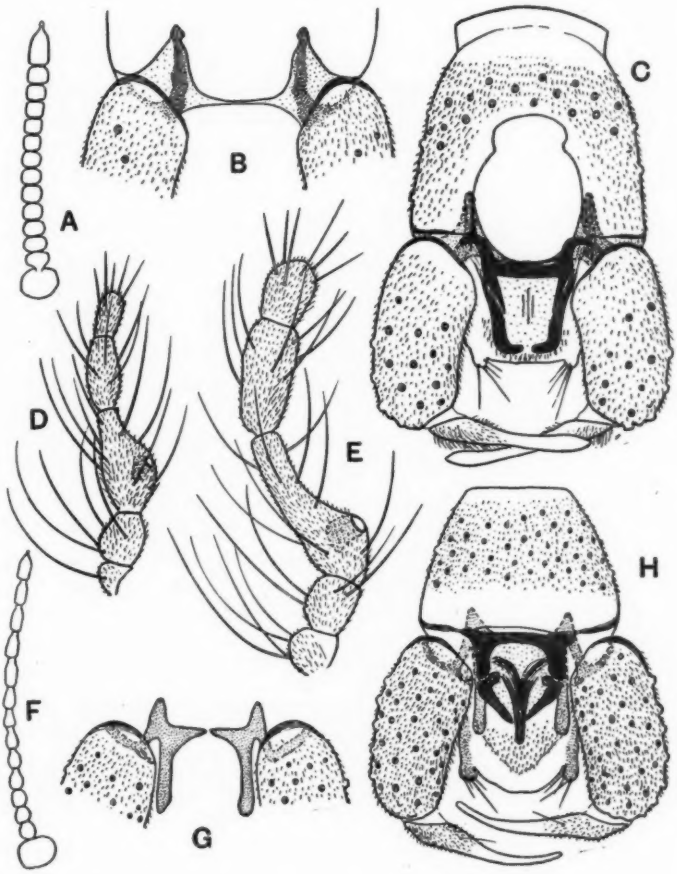


Fig. 9. *Thyridomyia frutetorum* Winn. **A**, female antenna. **B**, internal chitinisations of male hypopygium. **C**, ventral view of male hypopygium. **D**, left palp of female.

Forcipomyia (?) *murina*. **E**, left palp of female. **F**, female antenna. **G**, internal chitinisations of male hypopygium. **H**, ventral view of male hypopygium.

figured (Fig. 9, E–H) and discussed here on account of its obvious relationship with these genera, but the species must remain temporarily in *Forcipomyia* until the evidence of the immature forms becomes available.

CONCLUSIONS

The present study of the newly discovered early stages of *Apelma* and *Thyridomyia* n.g. has enabled the writer to establish the systematic relationship of the two groups to a much fuller extent than has been possible heretofore.

There has recently been a tendency to regard *Euforcipomyia* Malloch as a subgenus *Forcipomyia* (Edwards, 1923) and to suppress *Apelma* as synonymous with *Euforcipomyia* (Edwards, 1924); both these views were tenable when the adults only were considered, before the internal chitinisations of the male hypopygium were found to corroborate the classification by means of the early stages, as shown in this paper. Now, however, the writer has decided that Malloch's *Euforcipomyia* cannot be accepted until males of the type species, *hirtipennis*, have been described, since the principal distinguishing character, that of the long first tarsal segment, applies equally well to *Apelma* and a number of subgenera of *Forcipomyia*. It has therefore been necessary to erect a new genus, *Thyridomyia*, to include those species of Ceratopogonines, namely *palustris* n.sp. and *frutetorum* Winn. (with *aethiopiae* I. and M.), which may be separated from *Forcipomyia* by means of the following characters: (1) the greatly compressed basal flagellar segments of the female antennae (Fig. 8, E; 9, A); (2) the peculiar and distinctive form of the internal chitinisations of the male hypopygium (Fig. 8, H; 9, B); (3) the second hind tarsal segment about half the length of the first, or less; (4) the ventral position of the male sexual processes at the tip of the pupal abdomen; (5) the presence of papillae on all surfaces of the pupal abdominal segments (Fig. 7, J); (6) the reduced nature of the larval antennae, without a flagellar segment (Fig. 7, D, E, I); (7) the undivided condition of the larval prothoracic pseudopod, bearing many rows of minute hooks; (8) the complete absence in the larva of a cauda.

A close relationship with *Atrichopogon* is shown in the larva in its general appearance with spiny dorsal protuberances, its chaetotaxy, its lack of a cauda, and its chitinous plate on the dorsum of last abdominal segment. The ventral position of the male sexual processes of the pupa forms another link with that genus, as also does the presence of forward-running apodemes from the side-pieces of the male hypopygium.

The larvae of *Apelma* show their relationship with the terrestrial Ceratopogonines by their possession of anterior and posterior pseudopods, but apart from this they are very distinctive. The antennae are small, and apparently represent a step further in modification from the *Thyridomyia* type, both in reduction and in migration towards the mouth (Fig. 1, A, *an*). The head and body are strongly compressed dorso-ventrally (Fig. 1, B). The chaetotaxy is peculiar to the genus. The pupae are not flattened as the larvae. The ventral position of the male sexual processes of the pupa shows its relationship with *Thyridomyia* and *Atrichopogon* rather than with *Forcipomyia*. The articulated prothoracic horns of the pupa suggest affinities with the aquatic Ceratopogonines, as do also the setigerous papillae on all surfaces of the abdominal segments, though this peculiarity is shared by pupae of *Thyridomyia*.

A common European species, *murina* Winn., shows its connection with *Apelma* and *Thyridomyia* in the nature of the internal chitinisations of its male hypopygium, but other characters prevent its inclusion in either genus; it must therefore remain temporarily in *Forcipomyia* until the early stages have been discovered.

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(*MS. received for publication* 10. III. 1925.—Ed.)

STUDIES ON THE BIONOMICS OF MANGE MITES OF CATTLE.

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Sarcoptes of Cattle.

A young *Bull No.* 56904, infected with sarcoptic mange, was kept without treatment from v. 1923 to vii. 1924. During the summer of 1923 scrapings were taken frequently from this animal and numerous mites were obtained. These were examined and their external anatomy studied and described (see "Sarcoptes of Cattle," *Parasitology*, xvi. 255). In November, difficulty was experienced in getting eggs for study and in December the mites appeared to have gone. In 1924 scrapings were taken and examined once a week until June but no *Sarcoptes* were found, although many lice (*Trichodectes scalaris*) were present in each scraping. The neck of the bull showed bare areas with a hard, dry, scaly scurf.

As no mites had been found during about six months, when previously they could be obtained with little trouble, one feels justified in believing the case was spontaneously cured. The disappearance of the mites is attributed to the bull having been kept in a pen where he was exposed to sunlight, there being no overhead shelter.

On 5. xii. 1923, another bull (*Bull No.* 8566) affected with sarcoptic mange was brought to this Station. This animal had been given one treatment previous to shipment, therefore living mites were not found until about two months after its arrival. From this date, ii. 1924, the disease progressed steadily until viii. 1924 when the bull died from other causes. This bull was not exposed to sunlight whilst isolated.

Infection Experiments with *Sarcoptes* of Cattle on Various Animals.

Horse.

Horse No. 4 was placed in the pen with *Bull No.* 56904, affected with sarcoptic mange, and remained there from v. 1923 to vi. 1924. The animals were loose but were frequently seen touching each other when eating and drinking. Besides allowing this natural contact to occur, mites were placed on the horse.

On 3. v. 1923, scrapings from the bull were placed on the withers and at the root of the tail of the horse. On 10. v. scrapings, after examination for living mites, were placed upon the horse together with one egg and twelve

mites, including four females; the mites were placed individually at the roots of the hair on the withers. On 19. vii. twenty mites from *Bull No.* 56904 were placed at the roots of the hair on the withers and a fresh scab, with many living mites, was tied under the mane in front of the withers. Again, on 3. v. 1924, mites from *Bull No.* 8566 were individually placed and a scab containing living mites was attached to the withers where it remained in position for over twelve hours.

Although *Horse No.* 4 had mites in different stages and eggs placed directly upon it in suitable locations, and notwithstanding that the horse and infected bull were confined in the same pen together for over a year, no infection followed in the horse. During six months of this time mites were very numerous on this bull.

Result: Negative.

Sheep.

Sheep 1. On 10. v. 1923 a lamb was also placed in the pen with *Bull No.* 56904 and scrapings with living mites were rubbed into the hair on the face, nose and lips of the lamb. Some wool was rubbed loose on the throat following this procedure but no skin lesions or mites were seen. On 19. vii. twenty mites, mostly females, were placed on the face and a fresh scab with numerous living mites was tied to the wool adjacent to the face. The lamb was quite friendly with *Bull No.* 56904, it had a habit of running under the bull's neck if disturbed, so that actual contact was frequently observed. No infection followed although the mites had been placed on and around the site of sarcoptic mange in sheep. When killed, after a sojourn of three months in the pen with the infected bull, the lamb's skin was carefully examined for lesions and the face for mites but no sign of infection was seen.

Result: Negative.

Sheep 2 (Wether No. 676) was placed loose in a small shed with *Bull No.* 8566, suffering from sarcoptic mange. The bull was tied up. On 14. iv. 1924 scrapings from this bull were placed around the face and different parts of the wether's body, and again, on 3. v., scrapings containing living mites were secured to the wool at the top of the face and remained there for over twelve hours. Direct contact with the bull was not observed to take place frequently, nevertheless opportunity for infection by contact must have occurred repeatedly during the two months these animals were together; moreover, living mites were placed on the sheep. On 12. vi., Wether No. 676 was killed and the skin and especially the face were carefully looked over for lesions or mites. No infection was evident.

Result: Negative.

Rabbits.

Rabbit 1. In July 1923 twelve mites were placed around the base of the ears and scrapings from *Bull No.* 56904, containing many living mites, were rubbed into the fur of a rabbit. This was repeated on two other occasions, eggs

and mites being placed individually around the head and scrapings distributed over the rabbit's body.

Rabbit 2. Treated in a similar manner.

No skin trouble of any kind followed this effort to infect the two rabbits during the three months they were under observation.

Result: Negative.

White Rats.

Rat 1. In May 1923 nine mites, including one male, were placed at the base of the ears of a white rat—bred clean from the sarcoptic mange common on the ears, nose and tail of white rats. Furthermore, in July, twelve mites were placed on the rat but no infection followed.

Rat 2. Scrapings with living mites were placed at the roots of the hair around the ears and on the body of the rat on two occasions. No infection followed.

Result: Negative.

Cat.

A large black cat had nine mites placed at the base of the ears and two mites inside the ear on 8. iv. 1924. These were from *Bull No.* 8566. On 3. v. twenty-four mites of all sizes and scrapings with many living mites were placed around the cat's face and ears. When destroyed on 11. vi., no skin lesions or *Sarcoptes* could be found on the cat after careful examination.

Result: Negative.

Man.

A male and two females and an immature female *Sarcoptes* were placed on the skin inside a container fixed to the writer's arm[1]. The following day the male was dead and the others could not be found. Other attempts were made, but the mites would not remain on the skin, they sought the sides of the container. The longest period the mites were kept under observation was about 30 hours; during the daytime examinations were made every three hours. The mites made very little movement after the first hour and no irritation occurred. It seems evident, apart from this experiment, that *Sarcoptes* of cattle do not readily infest man, otherwise it is probable that at least a local infestation would have occurred during a year's experimental work with these mites. In taking scrapings from *Bull No.* 8566, a rather irritable animal, the material was occasionally upset over the operator's hand and arm.

Result: Negative.

VIABILITY OF *SARCOPTES* OF CATTLE AWAY FROM THEIR HOST.

Active Stages. When the mites are removed from their host, it appears more important to keep them damp than warm. In the incubator at 37° C. the mites were never observed to live longer than 3 days, while those kept

[1] The container was open at the bottom which was fixed to the skin by adhesive plaster. The container was closed by a screw lid in which a piece of glass had been cemented.

damp in an ice-box lived up to 11 days. The mites survived up to 7 days at room-temperature. When exposed to sunlight none survived to the second day and most of them were dead in a few hours.

Eggs. Of 111 eggs placed under different conditions only 25 hatched out. None hatched out in the ice-box after having been kept there a week or more, even when subsequently transferred to the incubator. At room-temperature 10 out of 38 eggs hatched after 3–8 days, and when kept at a like temperature in the dark 4 out of 18 hatched. In the incubator at 37° C., 7 eggs out of 18 hatched, 2 eggs hatched in the incubator after having been kept two weeks at room-temperature. As the time when the eggs were laid is unknown, the exact length of the incubation period under normal or experimental conditions still remains to be determined.

In the course of my experiments the active stages, after removal from the host, were kept in glass-topped metal containers or in glass cells on microscopic slides. Scrapings were kept in Petri dishes or in large glass-topped metal containers. The mites were assumed to be dead when no movement was observed on their being touched or turned over; as a further control, they were placed in the incubator for half an hour and again examined. Eggs were kept in glass cells on slides resting on supports over water, or moisture was supplied to the interior of the cell by wetted filter-paper placed over the cell, another slide serving as a lid and resting on the filter-paper.

EXPERIMENTS WITH *SARCOPTES* FROM CATTLE.

I. *The Effect of Sunlight, Darkness and Temperature upon the Active Stages.*

(*a*) *Sunlight (falling through window).*

Scrapings were collected from the Bull on 18. vii. 1923, the mites were isolated on the following day and exposed to sunlight. Some mites placed in an all-glass container all died on the 19th; of 6 ♀♀ kept dry, 1 was alive on the 20th, an identical result was obtained with 6 ♀♀ that were kept damp; all the mites were dead on the 21st.

Date of Collection	(*b*) *Darkness.*
26. vii. 23.	6 mites placed in drawer were all dead in 9 days.
5. iv. 24.	Scrapings placed in drawer, no living mites found after 9 days.
3. v. 24.	„ in black paper, in incubator, mites lived 3 days.
„	„ „ „ at room-temperature, mites lived 3 days.
18. vii. 23.	6 ♀♀ in box, damp, black paper covered, mites lived 3 days, all dead in 4 days.

(*c*) *Room-temperature.*

18. vii. 23.	Scrapings.	Adult mites all dead in 4 days, 1 larva alive after 5 days.
23. vii. 23.	„	Adults dead but 2 larvae alive after 4 days.
17. iii. 24.	„	Few mites present and all dead after 9 days.
10. vi. 23.	„	Mites alive after 7 days.
17. vi. 24.	„	„ „ „ 4 days.
18. vii. 23.	6 ♀♀.	2 alive after 3 days, both dead on day 4 (kept damp).

Date of Collection

(d) Room-temperature and in Incubator at 37° C.

18. vii. 23. Scrapings. 6 ♀♀ at r.t. 1 day, at 37° C. 1 day. All dead on day 2 (kept damp).
23. v. 24. 6 mites put in damp box at r.t. alive on day 3, then at 37° C. All dead on day 5.
— Several Exps. with mites kept at 37° C. dry or damp. Result, lived at longest 3 days.

(e) Room-temperature and Refrigerator.

18. vii. 23. Scrapings. 6 mites at r.t. 2 days, then in cold, all dead on day 4.
26. vii. 23. 6 mites, put in damp pill-box in cold, 1 still alive on day 11.
6. viii. 23. Scrapings, put at once in cold, mites alive on day 4, on day 5 at r.t., then cold again. Mites alive on day 8, all seemed dead on day 9.
10. iii. 24. Scrapings, in cold. Mites alive day 10, all dead on day 11.
5. iv. 24. „ 7 mites at r.t. 2 days, then cold, 1 alive on day 9.
20. v. 24. 10 mites, in cold, all dead on day 8.
„ Mites, in cold, living on day 6.

II. *The Effect of Temperature upon the Eggs.*

(f) Room-temperature.

Eggs kept in glass cells on slides over water.

18. vii. 23. 6 eggs, in open cupboard at 18–20° C., 2 hatched on day 8; rest transferred to 37° C., none hatched.
„ 6 eggs 1 hatched on day 8; rest did not hatch by day 16.
„ 7 „ 4 „ „ 8; „ „ „ „ 30.
21. vii. 23. 6 „ 1 „ „ 5; „ „ „ „ 14.
23. vii. 23. 6 „ 1 „ „ 3 and 1 on day 4.
24. vii. 23. 1 egg transferred to 37° C. on day 15, hatched on day 16.
„ 1 „ „ „ „ „ 16, „ „ 21.

(g) Incubator at 37° C.

Eggs kept in glass cells on slides, enclosing damp filter-paper.

18. vii. 23. 6 eggs, 1 day at r.t., then at 37° C., 1 hatched on day 2, 1 on day 3, 3 on day 6.
— 3 „ 1 hatched on day 2, 1 on day 3 and 1 on day 4.
10. iii. 24. 3 „ 2 „ „ 2, 1 „ 7.

(h) Refrigerator.

All eggs placed in the cold for 5 days or over and subsequently transferred to room-temperature or 37° C. failed to hatch during the time they were kept under observation, *i.e.* 5–30 days.

Infection Experiment I, with Psoroptic Mange in Cattle.

With the object of obtaining direct information regarding psoroptic mange in cattle, a heifer was purchased and placed in an open pen with a shed available for shelter. Active stages and eggs of *Psoroptes* were placed upon the heifer at the roots of the hair, and scabs with enormous numbers of living mites were attached and maintained in position upon the animal. Although this procedure was repeated over a period lasting from xii. 1920 to v. 1921, the heifer being kept isolated until vi. 1922, no distinct symptoms were observed.

Infective material was placed upon the heifer as follows:

10. xi. 20. Scrapings from known case of psoroptic mange placed on back and rump. No living mites seen in scrapings.

31. xii. 20. Scrapings containing many living mites and eggs. Individual mites were placed at hair roots and large scabs teeming with mites were attached to hair on withers and rump, the scabs remaining in position for 12 hours.

22. iv. 21. Scabs with many mites were tied on withers and rump and many living mites placed at hair roots. The scabs were rubbed off next day.

25. iv. 21. Scrapings left over from 22. iv. with living mites attached and rubbed into hair roots.

7. v. 21. Scrapings, scabs and living mites applied as before, hair over an area on withers clipped. Heifer secured for an hour to prevent interference with mites.

26. v. 21. Scrapings from known case containing many eggs but apparently no active mites were placed on heifer's back and the hair tied and gummed over them. Heifer secured during day to prevent interference with mites.

Note: 31. xii. 20. no evidence of mange. 8. i. no mites found. 11. i. 21. slight scab found high up on hair on front of withers but no mites. 7. iii. examination negative, heifer put on half feed to see if resistance lowered. 22. iv. heifer in poorer condition. 26. iv. heifer licking her back over its entire length. 7. v. no mange apparent, slight skin eruption but no mites found. 26. v. ditto. 1. ix. no symptoms observed to date except that heifer appears to lick her back more than normally on cold days. 16. x. condition good, no mange. 15. vi. 22. no symptoms of mange to date, heifer appears clean and sleek.

Result: Negative.

Chorioptes of Cattle.

It is possible that chorioptic mange in cattle is of more importance than hitherto supposed, moreover, it has been found in different herds suspected of having psoroptic mange.

On 23. iv. 1924 scrapings were collected from cattle, being taken from folds between the udder and thigh and from the furrow alongside the root of the tail. The scrapings were received on 26. iv. through the mail and were placed at room-temperature in a Petri dish covered with black paper to exclude the light. The scrapings were examined periodically. Many mites lived up to 26 days and one survived for 29 days.

Summary.

Infection experiments with *Sarcoptes* of cattle conducted upon a horse, two sheep, two rabbits, two rats, a cat and a man gave negative results. Active stages of the mite kept damp in the refrigerator lived 11 days, at room-temperature they lived 7 days, at 37° C. they lived 3 days, these being maximum periods observed. Eggs kept 5 days and over in the refrigerator subsequently failed to hatch when warmed; when kept at room-temperature they lived 16 days and hatched on being warmed; at 37° C. they survived 7 days.

Infection experiments with *Psoroptes* of cattle conducted upon one heifer gave negative results.

Chorioptes of cattle kept at room-temperature and protected from light survived 29 days.

(*MS. received for publication* 3. III. 1925, *condensed and summary added by G. H. F. N.*)

NOTES ON STRONGYLIDAE OF ELEPHANTS.

By G. WITENBERG.

(*From the Parasitological Division, State Institute of Hygiene, Warsaw.*)

(With 22 Text-figures.)

Owing to the courtesy of Docent W. Stefanski, University of Warsaw, I have had the opportunity of studying some Nematoda collected by him from the large intestine of an elephant which died in the Warsaw Circus.

The examination of these Nematodes allowed the identification of two species already known, *Murshidia falcifera* (Cobbold 1882) and *M. murshida* Lane 1914, and of two new ones, which I propose to name *Murshidia lanei* and *Pterygopharynx neveu-lemairei*, the descriptions of which are given below.

I wish to emphasize the fact that these identifications, especially the generic determinations, presented great difficulties, the diagnoses of the genera and their systematic positions being diversely interpreted by different authors; thus, Lane (1921) includes them in the subfamily *Oesophagostominae*, while Neveu-Lemaire (1924) considers them as *Cylicostominae*. As a matter of fact, both subfamilies are far from being accurately determined, every author using different criteria for their diagnoses.

Without going into details of the general systematics of the related divisions of the Strongyloidea to which the species examined by me belong, I find it necessary to establish for these a new subfamily *Murshidiinae*, with *Murshidia* Lane 1914 as the type-genus. The chief character of the worms of this subfamily is the peculiar construction of their mouth-parts, particularly the oval shape of the oral aperture, with the dorso-ventral axis longer than the lateral, and its specific armament in the form of two rows of leaflets, situated laterally and presenting the appearance of two fans.

Generally speaking, the structure of the mouth-parts provides the characters which in my opinion have the greatest significance in the systematics of the Strongyloidea; authors, therefore, who have neglected this fact and have laid stress on other characters (*e.g.* the structure of the male bursa) have been chiefly responsible for the confusion existing in the systematics of this group. This confusion exists not only in the diagnoses of the larger divisions, such as families and subfamilies, but also of the smaller ones, such as genera and species.

I propose to unite the subfamily *Murshidiinae* with the subfamily *Trichoneminae* Railliet 1916 in the family *Trichonemidae*.

Subfamily **MURSHIDIINAE.**

Diagnosis. Trichonemidae of medium size with a straight head and a mouth-cavity which is oval in cross section. The mouth-capsule has the shape of an oval ring, of which the dorso-ventral axis is longer than the transverse. The cuticular layer which paves the mouth-cavity splits, at different levels (according to different species), into narrow leaflets which form two rows corresponding with the longer curves of the mouth-oval and frequently projecting beyond the anterior body-margin. The base of the mouth-cavity leads to a funnel-shaped throat, which may or may not be provided with tooth-like processes. Four submedian head-papillae are generally well developed, the lateral ones are, on the contrary, generally very small.

The vulva is situated near the posterior extremity of the body. The ovejector consists of the following four parts: (1) vagina, (2) the median tube, (3) two separate tubes, and (4) two sphincter-like tubes. The two uteri run parallel cephalad.

In the male there are two similar spicules and an accessory piece.

Type-genus: *Murshidia* Lane 1914.

According to the existing literature, the genera included in this subfamily are comparatively poor in species, and do not differ widely from one another; they have been so inexactly diagnosed that it is possible to include some species in two different genera. This confusion may be explained by the fact that each of the authors (Lane, Khalil and Neveu-Lemaire) who gave diagnoses of the actually known genera based them on different criteria and not on a common principle. Thus, for instance, the genus *Pterygopharynx* Lane 1914, as shown by its name, was established by the author on the basis of the feather-like striations of the oesophageal folds as well as of other characters, particularly the construction of the dorsal rays of the male bursa. At the same time Khalil, ignoring the chief characters of this genus, proposed the genus *Memphisia*, the representatives of which must possess, besides all the characters of the genus *Pterygopharynx*, an additional ring-like thickening of the cuticle at the level of the head. When this cuticular thickening is not well developed it is obviously difficult to determine the generic position of the species.

Memphisia aziza Khalil 1922 may therefore be included in the genus *Memphisia* Khalil 1922 as well as in the genus *Pterygopharynx* Lane 1921. Similarly, *Henryella raillieti* Neveu-Lemaire 1924 may be considered as belonging to the genus *Memphisia*, and *Pterygopharynx anisa* Khalil 1922 to the genus *Henryella* Neveu-Lemaire 1924!

I consider it necessary therefore to modify the divisions of the subfamily Murshidiinae (as well as those of the subfamily Trichoneminae) on the basis of a definite and common principle. I have however found it difficult to carry this out actually for lack of the type specimens.

It is possible to agree, for the present, with Neveu-Lemaire who includes some forms belonging to the subfamily Murshidiinae in a tribe Pterygopharyngea, characterised by the fusion of the two outer rays of the male bursa. This tribe, therefore, includes the following genera: *Pterygopharynx* Lane 1921, *Memphisia* Khalil 1922, *Henryella* Neveu-Lemaire 1924 and *Buissonia* Neveu-Lemaire 1924.

The representatives of the genus *Murshidia* Lane 1914, which have tripled dorsal rays, may form the tribe Murshidiaea *nov. tr.*

In giving below descriptions of the species examined by me, I have drawn attention particularly to such anatomical details as have been treated superficially or totally neglected by other authors but which are to be considered as important from the systematic point of view. These concern chiefly the shape of the mouth-capsule as seen in various sections, the number and shape of the tips of the leaflets, the measurements of the different parts of the ovejectors, etc. It may be that some of the generic identifications of the species examined by me are incorrect; this is however due to the fact that the existing descriptions of the species and genera of the subfamily Murshidiinae frequently omit the details which are to be considered as essential and it was therefore not possible to make the necessary comparisons.

To illustrate the descriptions I have given detailed figures showing the principal characters of the worms dealt with.

Genus **MURSHIDIA** Lane 1914.

Murshidia falcifera (Cobbold 1882).

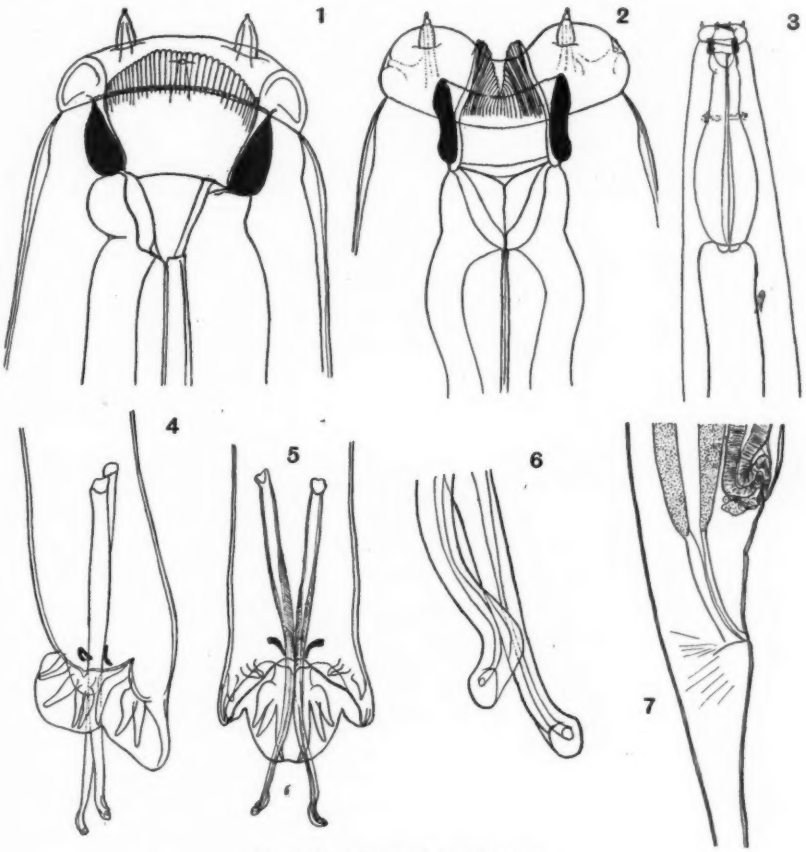
Figs. 1–8.

12 specimens were studied.

Males 25 to 27 mm. long; maximum breadth 0·8 to 1·0 mm. Females 25 to 32 mm. long, maximum breadth 0·8 to 1·0 mm. The body is cylindrical, finely striated, and gradually tapers in its last third. The head is rather flattened transversely, its dorso-ventral axis measuring 0·28 to 0·31 mm. and its transverse axis 0·26 to 0·27 mm. in ♂♂ and ♀♀. The oral aperture is surrounded by a distinctly separated mouth-collar, round in outline, from which project four high conical submedian papillae. The two lateral papillae do not project from the surface of the mouth-collar.

The deep oral cavity has the shape of an irregular funnel and is without any teeth. The mouth-capsule has the shape of an oval ring flattened from the sides, with the dorsal and ventral walls shorter than the lateral ones. In a dorso-ventral optical section the capsule appears thick (0·03 mm. in ♂♂ and 0·04 mm. in ♀♀) in its basal portion, it tapers entirely at its anterior margin and is 0·06 to 0·07 mm. high in males and 0·07 to 0·08 mm. in females. Consequently in this optical section the mouth-cavity appears wider in its anterior portion than at its base. On the other hand, in a transversel optical section the walls of the mouth-capsule appear higher (0·06 to 0·08 mm. in males and 0·09 to

0·12 mm. in females) and of equal thickness in both anterior and posterior parts. In consequence of this bilateral symmetry the outer diameter of the



Murshidia falcifera (Cobbold 1882).

Fig. 1. Head, lateral view.
Fig. 2. Head, ventral view.
Fig. 3. Anterior extremity, ventro-lateral view.
Fig. 4. Male bursa, lateral view.
Fig. 5. Male bursa, ventral view.
Fig. 6. Ends of the spicules.
Fig. 7. Female, posterior end, lateral view.

mouth-capsule measures 0·13 to 0·15 mm. in frontal section and 0·19 to 0·21 mm. in dorso-ventral section. The anterior margin of the mouth-capsule is not smooth but notched[1].

[1] The notched anterior border of the mouth-capsule is undeniably proper also to some species of the genus *Trichonema* Cobbold. From this peculiarity some authors may have conjectured that these species have an internal leaf-crown, to which the notches of the mouth-capsule bear much resemblance.

The cuticular layer lining the oral cavity splits from its middle into narrow leaflets which form two lateral rows corresponding to the two longer curves of the mouth oval, each containing 40 leaflets (80 in all). In the middle of each row the leaflets are long and project a little beyond the anterior end of the worm; at the ends of the rows the leaflets taper gradually and in the dorsal and ventral corners of the oral slit they are short and do not project from the anterior margin of the mouth-capsule. The leaflets have round ends and adjoin one another.

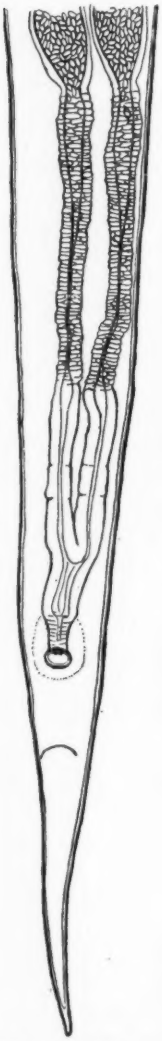


Fig. 8. Female, posterior end, ventral view.

The funnel-like base of the mouth-capsule is surrounded by the strong musculature of the short pharynx.

The oesophagus is mace-like in shape, 1·0 mm. long, and 0·3 mm. in maximum breadth.

The male bursa is comparatively short and the arrangement of its rays typical of the genus. All the rays are smooth. The medio-lateral and postero-lateral rays are closely parallel and turned aside from the externo-lateral ray. The three gradually tapering branches of the dorsal rays are unequal in length, the first is the shortest, the last the longest.

A short but distinct genital tubercle projects in front of the cloacal aperture.

The spicules are similar, 1·69 to 1·79 mm. long, 0·05 to 0·08 mm. thick in the proximal parts, whilst distally they taper gradually. Their ends are bent dorsally like the head of a golf-driver. The middle third of each spicule is provided with two incurved alae, ridged obliquely in a plumose fashion, forming a gutter; on the last thirds of the spicule these alae fuse, forming a canal which opens at the curved end of the spicule.

There is a small **S**-shaped, curved accessory piece, 0·05 mm. long, visible from the sides only. A telamon is present.

The posterior end of the female gradually tapers to a sharp point. The transverse anal slit is situated 1·59 to 2·18 mm. from the end of the body. The vulva is situated 0·69 to 0·83 mm. cephalad to the anus. Some specimens have a round, slightly prominent, button-like projection behind the vulva.

The bulky ovejector consists of the four following parts: (1) a muscular vagina, 0·13 to 0·2 mm. in length, always bent in the shape of an **S**, but this loop not extending caudad to the vulva; (2) a median tube, 0·2 to 0·5 mm. in length; (3) two separate tubes, each 1·05 to

1·51 mm. in length; and (4) two sphincter-like tubes, each 1·51 to 2·52 mm. in length.

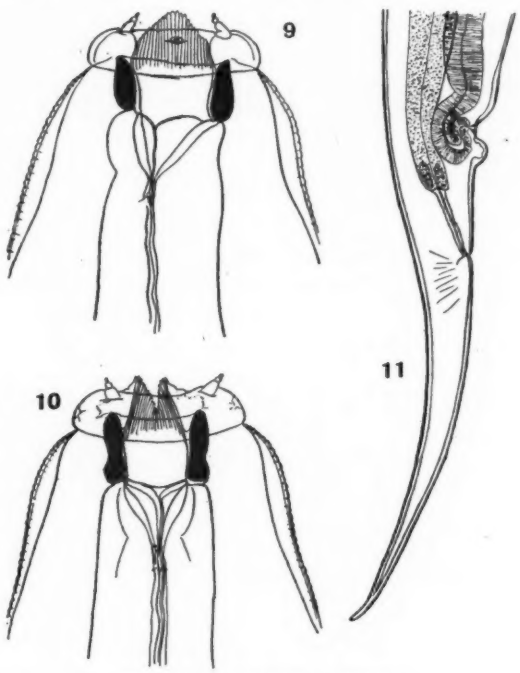
The ova are 0·084 mm. long and 0·041 mm. broad.

Murshidia murshida Lane 1914.

Figs. 9–11.

One female specimen was found in my material. Its description is as follows:

Length 27 mm.; maximum breadth in the middle of the body 0·7 mm., at the level of the head 0·26 mm. Cuticle delicately striated. The mouth-collar



Murshidia murshida (Lane 1914).

Fig. 9. Head, lateral view. Fig. 10. Head, ventral view.
Fig. 11. Female, posterior end.

is round in outline, but the convexity appears less on its lateral sides than on the dorsal and ventral ones. Submedian papillae well developed.

The mouth cavity is typical of the genus, that is to say it consists of three parts—the oval oral aperture bordered by the rows of leaflets, the mouth-cavity proper, and the throat.

There are 24 pointed leaflets in each row bordering the oral aperture (48 altogether). The middle leaflets are highest and project a little from the

anterior margin of the mouth-capsule. At the ends of the rows they become gradually shorter and scarcely reach beyond the anterior margin of the mouth-capsule.

The mouth-cavity proper is oval in cross section, since the mouth-capsule that determines its shape is wider in the dorso-ventral direction than transversely. The outer diameter of the mouth-capsule as seen from the side is 0·12 mm., viewed in front 0·11 mm. The optical sections of the walls of the mouth-capsule vary in shape in different parts; in dorso-ventral section they are oval, pear-like, 0·06 mm. high and 0·02 mm. broad; in the transversal section their shape is biscuit-like, 0·07 mm. high and 0·02 mm. in maximum breadth. The anterior margin of the mouth-capsule is denticulated.

The funnel-shaped throat is 0·05 mm. deep and entirely sunk into a muscular pharynx. It bears no teeth, but at the points of transition to the oesophageal slits there project the pointed slender ends of the oesophageal plates.

The oesophagus, which follows the pharynx, is bottle-shaped; its length measures 0·57 mm., its maximum breadth 0·05 mm.

The end of the body tapers gradually. The transverse anal slit is situated 2·26 mm. from the tip of the tail and 0·67 mm. caudad to the vulva. The vulva opens at the bottom of a funnel-shaped depression which is followed by a prominent, round, button-shaped projection, 0·11 mm. in diameter.

The ovejector consists of the four following parts: (1) the vagina, 0·5 mm. long, **S**-like and hung down beneath the vulva; (2) the median tube, 0·36 mm. long; (3) two separate tubes, each 0·97 mm. long; and (4) two sphincter-like tubes, each 1·0 mm. long.

The ova measure 0·072 mm. in length and 0·048 mm. in breadth.

Murshidia lanei n. sp.

Figs. 12–16.

Only one male specimen was found in the material.

Body cylindrical, 21 mm. long, 0·6 mm. in maximum breadth. The cuticle is delicately striated. The lateral parts of the mouth-collar are convex, the dorsal and ventral ones almost flat. Submedian papillae are well developed.

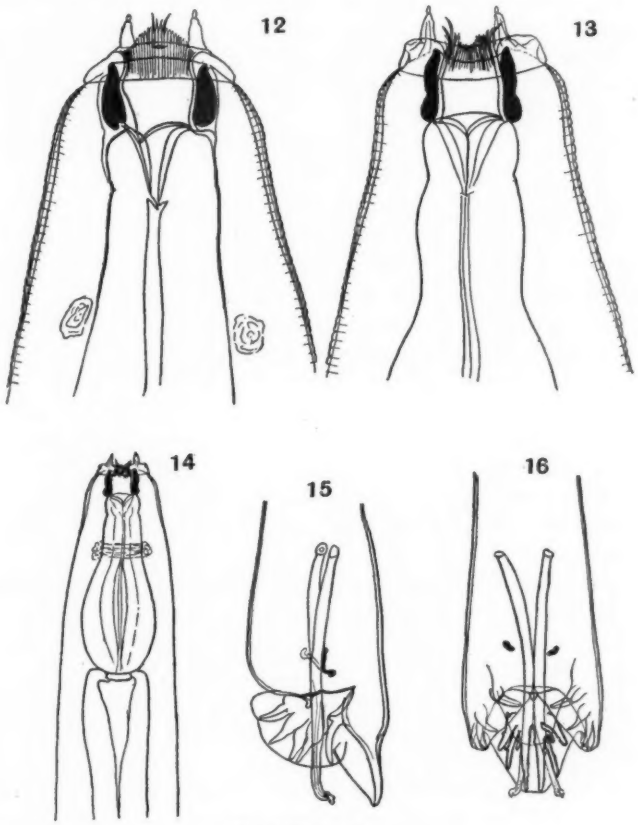
Each row of leaflets consists of 24 elements (48 in all). The leaflets are acutely pointed, they arise gradually from the end of each row to its middle, but the four central leaflets are exceedingly long and project considerably over the line. The shortest leaflets reach almost to the level of the anterior margin of the body, whilst the highest ones reach the level of the tips of the submedian papillae. Generally speaking, the leaflets of *Murshidia lanei* are comparatively longer than in other species of the same genus.

The mouth cavity is barrel-shaped, the anterior and posterior margins of the mouth-capsule being bent somewhat into the cavity.

In dorso-ventral optical section the mouth-capsule appears pear-shaped, 0·06 mm. high and 0·06 mm. in maximum breadth; in the transversel section it has the shape of an irregular biscuit, 0·07 mm. long and 0·01 mm. broad.

The throat, oesophageal funnel, is rather deep (0·06 mm.) and has on its bottom three little teeth projecting caudad.

The oesophagus has the shape of an elongated pear, 0·50 mm. long, and 0·35 mm. broad in its posterior part.



Murshidia lanei n. sp.

Fig. 12. Head, lateral view.
Fig. 13. Head, ventral view.
Fig. 14. Anterior extremity, ventral view.
Fig. 15. Male bursa, lateral view.
Fig. 16. Male bursa, ventral view.

The excretory pore is situated 0·36 mm. caudad to the posterior end of the oesophagus. Two very slender cervical papillae project 0·07 caudad to the excretory pore.

The male bursa is moderately long and slightly open. Ventral and lateral rays are smooth and symmetrical. Medio-lateral and post-lateral rays are closely parallel, their basal parts are very broad and their ends narrow. Externo-dorsal rays almost adjoin the post-lateral ones; they have smooth

edges, but the left ray is provided with a little sprout on its outer side. The dorsal rays have rough edges and many, more or less prominent, asymetrical projections.

The spicules are similar, without clearly visible alae; they taper gradually to the ends, where they bend dorsally; they contain a canal opening on their tips. There is a small spine behind the opening of this canal, on the tip of each spicule. The accessory piece, as seen from the side, presents the shape of an irregular **S**. Telamon present. A single small papilla projects in front of the cloacal opening.

Genus **PTERYGOPHARYNX** Lane 1914.

Pterygopharynx neveu-lemairei n. sp.

Figs. 17–22.

Three specimens of this species were encountered among the material—one male and two females.

The body is cylindrical, tapering anteriorly from the level of the oesophagus and, in the females only, posteriorly behind the vulva.

Male 23 mm. long and 0·6 mm. broad; females 25 to 28 mm. long and 0·7 mm. broad. The cuticle is finely striated at intervals of 0·006 mm.

The mouth-collar consists of two rings separated by a slight groove in which are situated the four strong submedian papillae. Each of the latter consists of three parts: a large basal portion, a small middle one and a fine terminal button. The lateral papillae do not project from the surface of the mouth-collar.

The oral aperture is in the form of an elongated oval, laced by two rows of leaflets; the latter originate in the anterior half of the walls of the mouth-cavity and have rounded tips. There are 20 to 24 leaflets in each row (40 to 48 in all). The highest, middle leaflets project somewhat from the anterior margin of the body, the others grow gradually smaller to the ends of the rows.

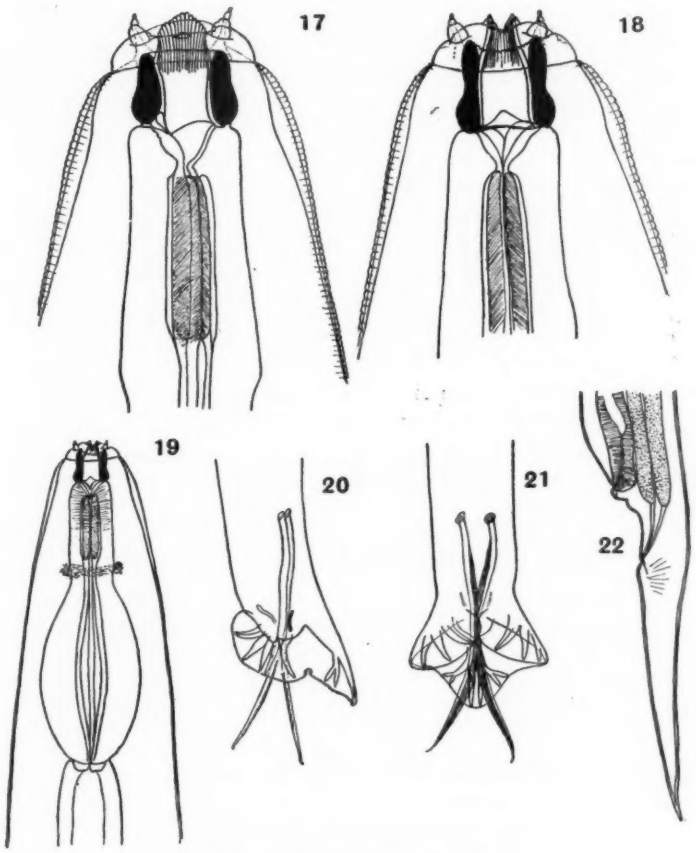
The oral cavity is almost cylindrical in shape. The section of the mouth-capsule when seen from the lateral side appears pear-shaped, 0·07 mm. in height, 0·02 mm. in breadth; when seen from dorsal or ventral side it appears biscuit-shaped, 0·08 to 0·09 mm. in height and 0·02 mm. in maximum breadth. The outer diameter of the mouth-capsule reaches 0·1 mm. The anterior margin of the mouth-capsule is denticulated.

The funnel-like throat is 0·06 mm. deep in the ♂ and 0·03 mm. in the ♀♀. No teeth are present, but a small tooth-like tubercle, 0·017 mm. high, perhaps a dorsal gutter, projects on to the base of the dorsal wall of the mouth-cavity.

The oesophagus is bottle-shaped, consisting of a short and narrow anterior portion (0·25 to 0·3 mm. by 0·11 to 0·13 mm.) and of an oval bulb, 0·3 to 0·48 mm. long and 0·22 to 0·28 mm. broad. The anterior part of the oesophagus is provided with three pairs of peculiar thick plates, obliquely striated in plumose fashion. These plates are to be distinguished from the similar ones described in other species of the genus, since they pave not only the initial

parts of the oesophageal slits but their whole length from the commencement to the level of the nerve-ring; they measure 0·17 to 0·19 mm. in length.

The excretory pore is situated 0·01 mm. caudad to the point of termination of the oesophagus. The delicate cervical spines project at the same level.



Pterygopharynx neveu-lemairei n. sp.

Fig. 17. Head, lateral view.
Fig. 18. Head, ventral view.
Fig. 19. Anterior end, ventral view.
Fig. 20. Male bursa, lateral view.
Fig. 21. Male bursa, ventral view.
Fig. 22. Female, posterior extremity.

The male bursa is unrolled, its dorsal lobe somewhat longer than the lateral lobes. All the rays are smooth and without distinct thickenings at their bases. The medio-lateral and post-lateral rays are parallel. The externo-dorsal rays are almost closely adjoining the post-laterals. The first dorsal rays are bifurcated in their distal halves.

The spicules are similar, 0·28 mm. long, thick proximally and tapering gradually to their terminations. They are provided with alae and have the shape of a feather. A small curved accessory piece and a telamon are present. A small genital tubercle projects in front of the cloacal opening.

The straight and sharply-pointed tail of the female measures 1·27 to 1·42 mm. The anus is protected by a large lip situated caudad. The vulva is placed 0·33 to 0·42 mm. cephalad to the anus, the region between vulva and anus is more or less depressed. Close in front of the vulva there projects an oval button-like papilla, 0·05 to 0·16 mm. The ovejector consists of four parts, as follows: (1) the vagina, 0·21 mm. long, without an **S**-like bend; (2) the median tube, 0·3 to 0·4 mm. long; (3) two separate tubes, each 0·3 to 0·4 mm. long; and (4) two sphincter-like tubes, each 0·5 mm. long.

The ova, as seen in the vagina, are 0·062 mm. long and 0·038 mm. broad.

The types of the new species are deposited in the Zoological Museum, Warsaw University.

I take this opportunity of expressing my deep gratitude to Dr W. Stefanski, to whom I am indebted for the material, so generously placed at my disposal, as well as to the Staff of the Institute, especially Dr L. Anigstein, for the privilege of utilizing the facilities of the Laboratory of the Parasitological Division for my studies.

My thanks are due to Prof. Charles L. Boulenger for his kindness in recasting the manuscript for press.

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(*MS. received for publication* 28. xi. 1924.—Ed.)

ON THE LIFE-HISTORY AND STRUCTURE OF THE EARLY STAGES OF SIMULIIDAE (DIPTERA, NEMATOCERA). PART I.

By I. M. PURI, M.Sc. (Punjab, India), Ph.D. (Cantab.).

(*From The Molteno Institute for Research in Parasitology.*)

(With Plates VIII, IX, and 6 Text-figures.)

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INTRODUCTION.

Adults of the family Simuliidae have been known in Europe for a very long time as very serious pests affecting both men and cattle, and there were many interesting legends, even up to the middle of the eighteenth century, explaining their origin from grottos in the mountains (Tömösváry). Fabricius (1784) for the first time found a *Simulium* pupa (probably that of *S. venustum* Say) and described it under the name *Tipula sericea*, but to Schönbauer (1795) we owe the discovery that the earlier stages (egg, larva and pupa) of *Simulium* (*Kolumbatczer-Mücke*) are to be found in running water. According to Nevermann and Wilhelmi (1920), Eichorn (1775) gives a figure of the larva (of *Simulium*), though without pointing out its relationship with any adult fly. Verdat (1822), Planchon (1844), Fries (1824) and Westwood (1848) are others of the earlier writers who deal briefly with the habits and external structures of the larva and pupa of *Simulium*, Planchon also dealing with a part of the internal anatomy. But their descriptions are so vague and their diagrams so

inaccurate that it is impossible to recognise the species they have described. Osten-Sacken (1870), McBride (1870) and Riley (1870, 1884 and 1886) are among the earliest observers of the habits and structure of the larvae of some of the American Simuliidae. Of recent years, owing to the suspicion that *Simulium* (adult) conveys the disease Pellagra to man, many valuable papers have appeared dealing with the early stages of these insects, especially from a systematic point of view; those of Johannsen (1903), Lutz (1909, 1910), Malloch (1914) and Pomeroy (1916) on the American, of Friederichs (1920, 1921) on the German, and of Edwards (1921) on the British species. Edwards' memoir is the only exact work on the British representatives of this family and has served as a useful guide in the preparation of the present paper.

CONCERNING THE GENUS *SIMULIUM*.

The genus *Simulium* Latreille, 1804, is universally recognised as valid to-day, although some confusion, happily temporary, was caused by the attempt to supplant the well-established name *Simulium* by that of *Melusina* Meigen 1800 on grounds of priority[1].

Recent authors have sought to sub-divide the genus *Simulium* as follows: Roubaud (1906) split the genus into two sub-genera, *Prosimulium* and *Eusimulium*, and Malloch (1914) adopted the former name in a generic sense. They had based this division on the structure of the second hind-tarsal segment and wing venation in the imago, and the structure of the cocoon and number of respiratory filaments in the pupa. But as there are intermediate forms—*S. meridionale* Riley and *S. subexcisum* Edw. in respect of the tarsi, *S. mutatum* Mall. and *S. pecuarum* Riley in that of wing venation, *S. pecuarum* Riley and *S. pallipes* Fries in that of the cocoon, and *S. lyra* Lundstr. in respect of the number of respiratory filaments, forming a complete and gradual transition between the two sub-genera—it seems superfluous to divide this homogeneous and well-defined family into sub-genera, so far as the European species are concerned. Enderlein (1921), dealing only with the adults, has divided the family into two sub-families and a number of genera, but Edwards (1923), while not agreeing to this breaking up of the family, says that "Most of the characters introduced by Enderlein for generic division (enlargement of the first hind tarsal segment in the male, size of the abdominal tergites in the female, and presence or absence of the small tooth on the female claw) are evidently subject to variation even in very closely related species, if not actually within the limits of one species." He suggests that division may be made into four groups (and not sub-genera), *Prosimulium* Roubaud, *Eusimulium* Roubaud, *Wilhelmia*[2] Enderlein and *Simulium* S.Str., adding, "in view

[1] Malloch (1914), in his paper, gives ample reasons against the adoption of the generic name *Melusina* Meigen in place of *Simulium* Latreille, and establishes the validity of the latter.

[2] From the accounts of Pomeroy (1920) of the early stages of some of the African Simuliidae, it seems probable that a further knowledge of the pupal stages of the other little-known species may reveal forms intermediate between *Wilhelmia* Enderlein and *Eusimulium* Roubaud, which are separated from each other only by the difference in the structure of the pupal respiratory filaments.

of the intermediate forms which undoubtedly exist between all of them it is very doubtful if anything is to be gained by maintaining any of them as sub-genera."

In the present paper I have followed the nomenclature given by Edwards (1921) in his paper on the British Simuliidae. My investigations upon the immature stages of British Simuliidae as well as upon some from Northern Europe (to be described in a subsequent paper) tend to confirm the conclusions arrived at by Edwards from his studies upon the imago.

HABITS OF THE LARVAE AND PUPAE.

Simulium larvae are usually found in streams and rivers where the current is strong, especially where the water falls over an impediment. Some species prefer a very rapid current, some a moderate current, whilst some appear more or less indifferent to the strength of the current. According to Edwards (1921), certain species prefer to attach themselves to plants with long filamentous divided leaves, while others fix themselves only to more or less smooth stones. The larva being sedentary in its habits, the main factor in the choice of its habitat, in every case, is a continuous flow of water surrounding it. Webster (1887) observes that the larvae fix themselves fairly deep in water (8 to 10 ft.), but personally I have never found them at a greater depth than 1 ft. and have frequently found them at less. When attached to aquatic plants they are always found nearer the surface of the stream than the bottom.

The larvae fix themselves to their support by their posterior end, which is flattened into a sucker-like disc. Under favourable conditions larvae may remain fixed to the same spot for some days, but usually they change their position frequently.

The mode of progression, which resembles the looping-movement of the larva of a geometrid moth, is described by Tonnoir (1923); but my observations differ slightly from his and can be described as follows: With its posterior end fixed to the basis, the larva stretches itself and selecting a suitable spot, applies to it a little of its sticky saliva, expelled directly from the salivary slit. The larva now fixes the thoracic proleg to this droplet and so becomes for a moment attached to the basis both by its anterior and posterior extremities. Simultaneously it applies some more saliva in front of the former spot and, freeing the posterior sucker, brings it forwards and fixes it in front of the thoracic proleg, which becomes detached at the same time. This process is repeated every time the larva moves. The statement by Riley (1886) that the larva moves backwards, is incorrect.

Simulium larvae cannot swim, but when disturbed they release their hold of the basis and float some distance with the current of water, hanging by a fine silk thread, one end of which is attached to the salivary slit and the other to the support. They can thus crawl back along this thread to their

former support, using for the purpose the proleg and mouth-parts (like a hand to hand rope-climb).

The method of feeding of the larva is very much like that described by Nuttall and Shipley (1901) for the larva of *Anopheles maculipennis*, when feeding at the surface of water. Fixed to its support by the posterior end, the *Simulium* larva assumes a more or less erect position, and turns the anterior part of the body, on the fourth abdominal segment as its axis, so that the head is rotated through an angle of about 100 to 160°. It then spreads out its fans, folding them alternately to sweep food particles into the mouth. At every sweep of the fans the labrum is drawn out and the mandibles and maxillae brought against each other. The food particles gathered in by the fans are retained in the funnel-shaped buccal cavity by the clusters of hairs present on the mouth-parts, when the water is strained through them. The fans act as strainers and do not produce whirlpools in water like the "mouth-brushes" of *Anopheles* larvae. Every now and then the bristles on the mandibles are passed through the filaments of the fans and so clean the latter of adherent particles. Occasionally the larva swallows particles scraped by means of its mandibles from the surface on which it is fixed.

Food: The statements of different authors vary as to the nature of the food of the larvae. According to Fries it consists of vegetable matter. Planchon found spherical animalcules and in some cases Infusorians like *Vorticella* in the gut of the larvae. Riley (1886) says that they feed on minute Crustacea and other small animalcules, but they do not disregard vegetable food, such as Diatoms. Kellogg (1901) and Miall (1912) found siliceous shells of Diatoms in the gut and Miall also found fragments of small Crustacea. Pomeroy considers that they thrive best in streams containing the largest proportion of organisms like *Euglena viridis* and *Spirogyra*.

The intestines of larvae taken from the River Cam, about Cambridge, were always found filled with shells of Diatoms, with here and there pieces of minute Crustaceans, and a fair amount of other organic matter. Larvae of different species collected from the same locality always show more or less the same type of gut contents. They feed on all kinds of minute fresh-water animalcules and algae. In an exceptional case the gut of a larva contained over twenty complete head-capsules of small *Chironomus* larvae. I attribute the different statements of the authors previously quoted, regarding the food of the larvae, to the insects they examined having come from different localities.

The larvae of two species of *Simulium* were reared by me from eggs in the laboratory at Cambridge. Both the larvae and adults of one species (*S. aureum* Fries) thus reared, attained a normal size, while those of the other (*S. erythrocephalum* Deg.) were much smaller, even less than three-quarters the size of specimens met with under natural conditions. The larvae of both these species often occur together in the same stream. In the aquaria they were reared under similar environmental conditions and at the same time,

therefore it seems that the food supplied was more suitable in the one case than in the other.

Colour: Pomeroy and other writers state that the *colour* of the larvae is inconstant and that it varies with the food. My observations, however, do not support this conclusion. There is no doubt that owing to the larvae being more or less transparent their gut-contents show through the body-wall, thus modifying their apparent colour when superficially examined, but the main or actual colour of the larva is due to a layer of pigmented fat-body cells beneath the epithelial lining of the body-wall. That the nature of the food has no effect on the colour of the larva is proved by the circumstance that *S. aureum* and *S. erythrocephalum*, though raised on the same food and under the same conditions, developed two different colours, the former golden brown, the latter pinkish-grey.

Respiration: *Simulium* larvae need much oxygen, and consequently, when transferred from a running stream to stationary water, they die in about five to six hours from lack of oxygen. On the other hand they can live, even for three to four days, when loosely wrapped up in a piece of wet cloth. If placed in a jar full of water they migrate to the edge of the water where most oxygen is available, and very often extend their anal gills out into the air, the gills being covered only by a thin film of water. Their need for oxygen is clearly shown experimentally: About fifty larvae were placed in a small aquarium full of rain-water where they settled down at the water's edge. On bubbling air through water, to one side of the aquarium, it was observed that all the larvae gradually migrated and settled on the side over which the air bubbles were passing. On moving the aeration-tube to another part of the aquarium all the larvae migrated to that region and fixed themselves in the path of the air bubbles. No speed at which the air was bubbled through the water was excessive to them and they very often fixed themselves to the end of the aeration-tube. When air was bubbled through a porous block of wood, the block always became covered with larvae which often pupated upon the wood.

Rearing: Many investigators have failed to rear *Simulium* from egg to imago in the laboratory. Martini (1921) only raised them from the egg to the second-stage larva. He describes an elaborate aquarium which he employed for the purpose and insists that a vertical and constant flow of water is required.

I have reared *Simulium* from egg to adults and find that no special arrangement for the aquarium is necessary. The aquaria used were inverted bell-jars measuring about 40 cm. in depth by 40 cm. in width. They were nearly full of rain-water which had a greenish colour due to a minute green alga (? *Chlorella* sp., *ca.* 1μ in size) on which the insects fed throughout their larval life. Air was constantly bubbled through the aquaria by means of an *aeration pump* (supplied by Messrs L. Hecht and Co., Berlin, one pump was found enough for three or four aquaria). Over these aquaria fine muslin nets were arranged to collect the adults when they emerged. Constant aeration and plenty of food are all that are essential for the growth of these larvae.

Duration of Larval Life.

Opinions differ regarding the duration of larval stage in *Simulium*. Verdat (1822) and Kollar (1848) thought that *S. ornatum* (described as *S. sericeum*) took four to five months to develop from egg to adult in winter or summer, the winter brood hibernating in the larval stage. Tömösváry (1892) thought that the larval stage of the columbaczer fly at Banat lasted 6–8 weeks in June and July and that winter is passed in the pupal stage. Philips (according to Coquillet, 1896) observed that the larval life of *S. venustum* Say in the United States, lasts about four weeks in summer but is longer in winter, and Hunter (1913) has observed like periods in the case of *S. vittatum*.

My rearing experiments with *S. aureum* and *S. erythrocephalum* show that in both these species the larval stage lasts 4–5 weeks in summer (August, 1923 and 1924). I have made no observations in winter. In those species which hibernate as larvae, this stage must last for months in winter, but four to five weeks appear to be the normal duration during the summer months. McBride, Philips and Hunter believe that the duration of the larval stage varies with the velocity of the water, but my observations do not support their view. Larvae (of one species), which had emerged from eggs about the same time, were kept in two separate aquaria. The speed with which air was bubbled through these aquaria (and consequently the velocity of the water-currents) was markedly different but still the larvae pupated at more or less the same time.

Larval Moults.

According to Meinert (1886), Horvárth (1884) thinks that there are four larval moults. Tömösváry says that there are four moults and a fifth when the larva pupates; Aigner-Abafi (1903) shares this opinion. Edwards (1920–1), by noticing the size of the various larvae of *S. latipes*, collected by him, was able to count six larval moults (pupation taking place at the sixth moult), and Cameron (1922) observed the same number by measuring the effete posterior suckers in the case of *S. simile* Mall.

By following up the entire larval development of *S. aureum* and *S. erythrocephalum* from day to day I have also found that pupation occurs at the sixth moult. Healthy larvae moult every 4–7 days till they pupate.

Method of ecdysis. Strickland (1911) thought that ecdysis of the head-capsule only and not of the rest of the body takes place, and Planchon advanced the same curious view especially about the last larval moult, when the larva pupates. Pomeroy has, however, shown that the entire larval skin is moulted.

At the time of ecdysis a slit appears on the head along the lateral and the posterior border of frons-clypeus, the slit extending (downwards) between the head and thorax. The head and thoracic proleg are then withdrawn, the proleg is fixed to the basis and the body gradually drawn out of the rest of the skin,

which remains where the larva was fixed at the time of moulting. The head-capsule is not cast off separately from the rest of the skin, as is generally believed, but on account of the thin connection between the two, the former is washed away by the current of water after ecdysis. If a larva is allowed to complete its moult in stationary water, it is seen that the head-capsule is connected to the rest of the skin near the median ventral line.

Formation of the cocoon and the last larval moult. Authors differ regarding the manner in which *Simulium* larvae form their cocoon. According to Johannsen (1903), Miss Philips found that the anterior end of the cocoon is spun first, while Friedrichs says that a larva first weaves the posterior part and then putting its body into it completes the anterior portion. Westwood (1848), Meinert (1886) and Miall (1912) believed that the cocoon is formed as a closed elongated chamber, the anterior part of which falls off as a lid when the larval skin is cast off. Tonnoir has recently described in detail the mode of formation of the cocoon and the pupation process of *S. tillyardi*.

My own observations on the three species *S. nölleri*, *S. erythrocephalum* and *S. aureum*, differ in some respects from Tonnoir's description of the formation of the cocoon. In all these three species the fibres forming the cocoon are laid down at random and the network is very irregular[1]. A larva takes from 40 to 60 minutes to build its cocoon. When the cocoon is completed, air appears in the future pupal filaments (the black spot on each side of the prothorax becoming silvery in appearance) and the larva fixes its two extremities outside the cocoon, doubling itself in the form of a U. After about 10 minutes' rolling in this position, the posterior end of the future pupa begins to retract from the skin of the larva, and in another 4 to 6 minutes, the mesothoracic region swelling up considerably, the larval skin bursts, as in other larval moults. The pupa then frees itself from the larval skin and gradually makes its way into the cocoon. The whole process, from the beginning of the cocoon-formation to the completion of ecdysis, takes 75 to 90 minutes. There are always a number of fibres stretching in front of the opening of the cocoon, probably representing the lid of Westwood and others. These fibres save the newly formed pupa from being carried away by the current of water, as at that time the pupa lies more or less outside the cocoon to which it is not yet fixed by the hooks on its body. Once a pupa has entered the cocoon, it is fixed to the latter and never leaves it of its own accord, as has been wrongly described by McBride and Riley (1886). At the time of emergence of the imago the anterior part of the pupa protrudes from the cocoon much more than before, but this is due to the stretching of the abdominal region, the posterior end of the pupa remaining fixed to the cocoon by means of hooks provided for the purpose.

[1] The larvae I have studied proceed to build their cocoons as follows: (*a*) The larva at first spins a loose network of threads on the substratum between various points laid down at random on the flat surface just behind it. (*b*) Continuing, it spins threads passing dorsally over its body, whereby the cocoon becomes clearly defined, as a loose basket. (*c*) It now frees itself and becomes fixed at the cocoon-opening and thickens the network from the inner side.

Duration of Pupal Life.

According to Newstead (1907–8) the pupal life lasts 2–6 days, while other authors say that it lasts 2–3 weeks.

I find that the length of the pupal stage varies greatly with the temperature; within limits, the higher the temperature, the shorter is the duration of the pupal stage. At the end of July (1922) pupae of *S. nölleri* hatched out in about 5 days, while in the beginning of October of the same year they took 10 days. Early in November (1922) two lots of *S. nölleri* pupae, formed about the same time, were subjected to different temperatures, one lot being placed in a room at about 16° C., while the other lot was placed in the open, at an average temperature of 3·8° C. Pupae hatched out in 5 days in the room, while those placed outside took from 13 to 15 days. According to Pomeroy the maximum duration of the pupal stage in *S. venustum* was 9 days, at an average temperature of 2·2° C. It appears from these observations that either the duration of the pupal stage varies in different species of *Simulium* or there is some other factor affecting the development of the pupa in addition to temperature.

For hatching pupae only, the method suggested by Newstead (1907) is very simple and has been found useful. It consists in removing pupae from the stream and placing them in a jar, whose atmosphere is moistened by the addition of a few drops of water. Under these conditions they will successfully complete their transformation into adults.

Parasites of *Simulium*.

Various Protozoan parasites have been described from *Simulium* larvae. Léger (1897), Chatton and Roubaud (1909), and Debaisieux (1920) have found, respectively, a Myxosporidian, an Amoebidium and Caelomycidian parasites inside larvae in France, and Strickland (1911, 1913) has described two sporozoan parasites in larvae from North America. Strickland has also described a Nematode of the genus *Mermis*, parasitising larvae of *S. hirtipes* in America and this has also been found, though very rarely, in this country, by Swinton (1913) and Edwards.

While rearing larvae in the laboratory, from eggs collected from the River Cam, a certain number became infected with a *Microsporidian* parasite. I am not able to say how the infection took place but it was discernible only during the advanced larval stages, when milky-white masses could be seen within the body of certain specimens. The imaginal discs of such larvae were very small, while in healthy larvae, at the same stage of development, they were well-developed. The obvious effect of these parasites on the host was to lengthen considerably the larval life, and it was found, as already pointed out by Strickland (1913), that the parasitised individuals failed to pupate.

EGGS.

Eggs of Simuliidae (Text-fig. 5, *B*) have an elongated triangular form, with broadly rounded angles (*a*). The eggs of the three species, which I have met with, are found on the upper surface of leaves of water plants, submerged in water. Although I have not observed the process of oviposition, it seems clear from the position in which the eggs are found that they must have been laid under water[1]. The eggs occur in large masses placed side by side in a single layer, and with the naked eye, appear like a brown rust on the leaves. That these masses are laid by more than one female, is obvious because the batches of eggs, lying close together, hatch at different times. When freshly laid the eggs are cream coloured, but as development proceeds their colour changes to golden brown and then to deep brown. The eggs gradually become more or less transparent and about 24–36 hours before hatching the eyes of the future larva are seen as black spots on each side of the anterior end. A little after this a dark spot, the *egg-burster*, makes its appearance on the dorsal side between the eyes, and by this time the outline of the coiled larva can easily be seen through the transparent egg-shell.

According to Edwards (1921) the eggs of *S. equinum* are devoid of hard shells and are enveloped in a somewhat transparent gelatinous substance, whilst in *S. aureum*, which has hard-shelled eggs, no such gelatinous substance occurs. In the latter case my observations, based on rearing experiments from egg to adult, do not confirm those of Edwards. The eggs of *S. aureum* are also covered by a gelatinous substance.

MORPHOLOGY OF LARVAE AND PUPAE.

The external and internal anatomy were studied in detail in *Simulium nölleri* Fried. and are here described, while in the case of the other species only the specific characters have been dealt with.

(1) Simulium nölleri Friedrichs, 1920.

= *S. subornatum* Edwards, 1920.

(A) Larva.

External Anatomy.

The description of the larva falls under three sections: (1) the head, (2) the three thoracic, and (3) the eight abdominal segments.

The Head.

The cylindrical chitinous head-capsule is barrel-shaped and about as long as it is broad. It forms an angle of about 150° with the thorax. Its antero-

[1] Oviposition under water has been observed by Britten and Edwards in *S. equinum* as follows: The female enters the water where the current is not very strong, walks along a twig to a depth of several inches, with her wings wrapped round her abdomen, thus enclosing a bubble of air. She then lays her eggs on a twig or leaf. Having oviposited, she releases her hold and rises to the surface of the water.

dorsal surface slopes downwards and passes into the labrum, while the lateral and ventral sides end abruptly to give attachment to the mouth-parts. The postero-ventral border is incompletely chitinised. The head-capsule appears to consist of three plates, one medio-dorsal and two lateral (epicranial). The median plate, the *Frons-Clypeus*, covers the dorso-median portion of the head, being separated laterally from the *Epicranial plates* by a narrow but clearly defined suture, along which the head-capsule bursts at the time of ecdysis. At the anterior end, the frons-clypeus bears the labrum and the pair of fan-shaped appendages. The epicranial plates form the sides and ventral portion of the head-capsule. The anterior border of the epicranial plates is produced forwards in many places to give attachment to the mouth-parts and is much thickened in the mandibular region. From the upper end of this thickened portion, a strong apodeme (Pl. IX, fig. 24, *t.t*) runs inwards and downwards to support the hypopharynx and mandibles. This apodeme is the only remnant of the elaborate tentorium found in many other dipterous larvae. The posterior border of each epicranial plate is strengthened by a thick chitinous rim which ends in a large thickened area[1] situate ventrally. The epicranial plates fuse along the medio-ventral line only in the anterior half and remain apart posteriorly, leaving a fairly wide bay in the ventral wall of the head-capsule.

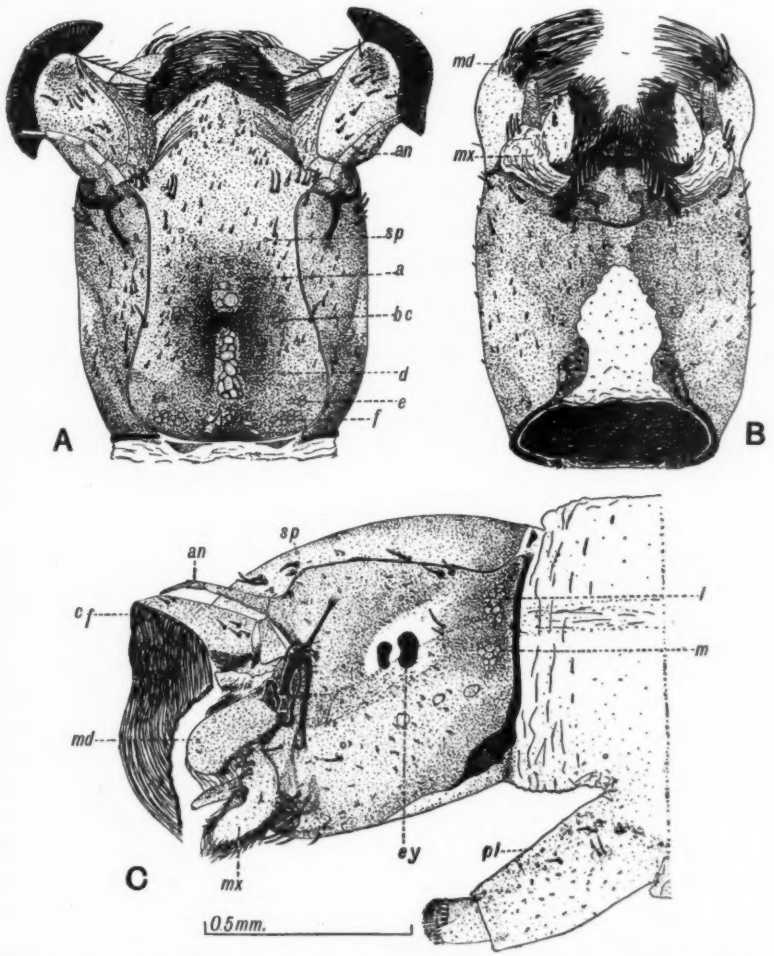
Eyes: A pair of black pigmented kidney-shaped eye-spots (*ey*, Text-fig. 1) are situated on each side of the head nearly in the centre of the epicranial plate. The paired eye-spots lie close to one another; the anterior, which is smaller and at times, varies in form.

On the head-capsule are a number of disc-like areas arranged in groups. They mark the places of attachment of muscles in the head and follow a definite distribution in all larvae. These discs are uniformly pigmented and are lighter in colour than the surrounding parts. On the dorsal surface of the head there is an anterior elongated group (*a*, Text-fig. 1) (for the epipharyngeal muscles) and a little behind this is a pair of small groups on each side (*b c*) (for the various pharyngeal muscles). Posterior to these is a large median group (*d*) and a pair on each side of smaller ones (*e* and *f*) near the posterior edge of the frons-clypeus and these mark the attachment of the strong muscles of the fan-shaped appendages and the retractor pharyngeal muscles. On the sides of the head the only group of discs clearly made out in this species are a pair (*l* and *m*) lying near the posterior border and indicating the attachment of the mandibular muscles. The place of attachment of the maxillary and the labial muscles is not well defined. Just behind the posterior convex border of the clypeus are a pair of very small strongly-chitinised sclerites to which are attached the *post-cerebral-oesophageal* muscles.

The pigmentation of the head shows a definite pattern in all larvae; the depth of colour varies from light brown to dark brown, depending on the time passed since the preceding moult. Dorsally, between the four groups of disc-like areas, which are arranged in the form of a cross, the frons-clypeus is deeply

[1] This may be another remnant of the tentorium, or of a branch thereof.

pigmented and shows a diffuse H-shaped spot of darker colour along the median line. Near its posterior border is another dark spot from which the pigment spreads on each side and surrounds the two posterior pairs of groups



Text-fig. 1. *S. nölleri*, Head of larva. *A*, Dorsal view (filaments of the cephalic fans cut off). *B*, Ventral view. *C*, Lateral view with the thoracic proleg.

a, *b c*, *d*, *e*, *f*, *l* and *m*, groups of discs; *an*, antenna; *c f*, cephalic fans; *ey*, eye-spots; *md*, mandibles; *mx*, maxilla; *p l*, proleg; *s p*, sensory pit.

of discs on the frons-clypeus. On the sides of the head there is a curved stripe of pigment dorsal to the eye-spots, in the form of an eye-brow, which is connected with a large pigmented area lying behind the eyes.

The head bears twenty pairs of simple pointed sensory hairs and five pairs of pits, distributed as shown in Text-fig. 1. Besides these there are numerous micro-setae which follow no definite arrangement and are scattered all over the head.

Appendages of the head.

The Antennae[1] (Pl. IX, figs. 14 and 15), arising in the dorso-anterior angle of the epicranial plates, from a slightly raised base, are cylindrical and consist of four segments. They have some appearance of being six-segmented, but the division between segments 2–3 and 3–4 is very indistinct and only superficial. The first segment is about half the length of the second and the third is a little longer than the first. The fourth or terminal segment is pointed and short. The antennae taper gradually from the base to the distal end of the second segment and the third segment, which is much narrower than the preceding one, is practically of uniform thickness throughout its length. The second segment bears at its distal end, on the inner side, two small stumpy sensory setae (*s.p*, fig. 15) both of which are supplied by a single nerve from the antennary ganglion lying at the base of the antenna.

Cephalic fans (Pl. IX, figs. 11–13). Just in front of the antennae are a pair of appendages which, when spread out, look like a fan on each side of the head. The stalk of each fan consists of two segments (Text-fig. 1, *A* and *C*, but only one shown in Pl. IX, figs. 11, 12). The basal segment, in the form of a rectangular plate upon the posterior surface of the fan, articulates with the epicranial plate, while the broad second segment, which forms the major part of the stalk, articulates with the frons-clypeus on the inner side. The second segment bears along its distal border a row of strong curved filaments which when spread out form the palm of the fan. These filaments are flattened vertically near their base and their ventral margins are produced so as to overlap the filament behind, when the fan is open. Along the distal two-thirds, each filament bears ventrally a regular fringe of short hairs interspersed at regular intervals by stouter and longer ones (Pl. IX, fig. 13). Besides these long filaments there is a row of 10 to 12 simple, elongated setae and another S-shaped row of plumose ones, both on the ventral side of the fan. The chitin of the ventral or anterior wall of the stalk is variously thickened and produced inwards into strong apodemes for the attachment of the strong muscles of the fans (Pl. VIII, fig. 1).

Planchon described the fans as modified lateral parts of the labrum, but Meinert says that they are the much-developed sides of the second metamere of the head, which are turned downwards on the segment in other dipterous

[1] The antennae of the larvae of Simuliidae always have a very small terminal portion, which Meinert (1886) and Friederichs regard as merely a sensory seta; Planchon, Riley, Edwards and others, however, regard it as a segment. Consequently some confusion has arisen as to the number of antennal segments in the various species. In the present paper the terminal portion is regarded as a segment.

larvae. Unfortunately Mecnikow (1866) and Graber (1889) and, according to Strickland, Kölliker (1842), in their embryological studies on *Simulium* larvae, do not explain these structures, though I have found them to be present in the youngest larvae, even in those dissected from eggs a few hours before hatching. However, the fact that the fans are innervated by the same nerves that supply the labrum, tends to support Planchon's view, above mentioned.

In the larvae of CHIRONOMIDAE, a pair of moveable processes arise from the ventral surface of the labrum and, on account of their position in front of the mandibles, Goetgebeur (1912) has named them the "Premandibles." From their insertion on the labrum and their innervation he concludes that they are parts of the labrum, and is of opinion that they represent a pair of appendages belonging to a special segment of the head. He goes on to say that the labrum, like the labium, is formed by the fusion of a pair of appendages, remnants of which are seen as his "Premandibles" in *Chironomus* larvae, and erroneously states that the labrum and his "Premandibles" are innervated by the Tritocerebrum, the part of the brain which supplies the premandibles in the COMPODIIDAE. The labrum in Insects is innervated from the Protocerebrum (Packard, 1909; Berlese, 1909) and in *Simulium* larvae the nerves of the labrum, of the cephalic fans and the frontal nerves[1] arise together as a single nerve on each side from the Protocerebrum. There is no doubt that the *Premandibular Organs* of dipterous larvae are modified parts of the labrum and are not homologous to the Premandibles of *Campodiidea*, so that the name ("Premandibles") given to them by Goetgebeur is rather misleading. Most probably these organs (in Dipterous larvae) are secondary structures and it appears that their evolution has followed two different lines: (*a*) where they lie outside the buccal cavity, the comparatively simple mouth-brushes of the larvae of Culicidae[2] lead up to the very complicated cephalic fans of *Simulium* larvae; (*b*) where they are more or less within the buccal cavity, the simple rod-like processes, found in some *Chironomus* larvae, lead to the divided "Premandibles" of the larvae of *Dasyhelea* (according to Saunders, 1924, p. 174, footnote).

Labrum and Epipharynx (Pl. IX, figs. 21, 22 and 29). The labrum is nearly semicircular in shape and is directed vertically downwards, overhanging the mouth-opening. Along its distal border it has short stumpy tooth-like projections, two of which on each side are longer and stouter than the rest (Fig. 29). Its dorsal or anterior surface is covered with a large number of long simple setae and also bears on the median line an elongated patch of strong distally-directed hooks (*g.h*), with broad scale-like bases. The ventral surface of the labrum (and not the dorsal, as Johannsen, 1903, has stated) is reinforced by

[1] Frontal nerves from the two sides unite to form the median *Frontal ganglion* of the visceral nervous system.

[2] These *mouth-brushes* resemble the cephalic fans of *Simulium* larvae, both in position and to some extent in structure and according to Howard (1912) and Thompson (1905) are only lateral parts of the labrum.

a strong T or Y-shaped sclerite, with the base of its vertical limb much flattened; on this surface there are three or four transverse rows of long branching setae which are directed into the mouth opening.

The ventral wall of the labrum is continued backwards as a soft plate, the *Epipharynx*, bounded posteriorly by a rim of strong chitin. The epipharynx forms the dorsal wall of the mouth-opening and has a number of transverse rows of short setae directed backwards. Near its anterior border is a patch of strong chitin for the attachment of the median epipharyngeal muscle (Pl. VIII, fig. 1, *ep.m*).

Mandibles (Pl. IX, figs. 16, 17 and 20). The mandibles are placed below the cephalic fans and move horizontally almost continuously when the larva is fixed by its posterior end. Each of them is formed of a stout, somewhat elongated piece with the outer lateral margin rounded and the inner rectilinear. It is articulated to the side of the head at a point where the border of the epicranial plate is thickened into a strong rim. Below the apex of each of the mandibles on the inner lateral margin there are three strongly chitinised black teeth (*t*) lying one above the other, the ventralmost being about twice the size of the other two, which are about equal. On the ventral side of the largest tooth, along its inner margin, there are three small teeth (*s.t*) of the same shape though much lighter in colour. Proximal to these teeth there is a row of about 10 to 12 elongated bristle-like teeth (*b.t*) decreasing in size from before backwards; and external to this row are two other irregular rows of smaller, pointed, teeth, one behind the other, the inner row having about 6 to 8 and the outer 4 to 5 teeth. The inner border of the mandibles in the region of the bristle-like teeth is produced into a broad flattened tooth-like process (*t.p*) immediately followed by another very small one; each of these being even lighter-coloured than the bristle-like teeth.

The relative size and the number (mostly three) of light-coloured teeth, the number of the bristle-like teeth in the various rows and the shape of the two flat tooth-like processes serve as very good specific characters for some species.

The mandibles bear clusters of long setae of various types. Some are arranged in the form of a bush (*b*) (near the apex), others in layers spreading out like a fan (on the inner border), while still others are placed in a row forming a fringe. The thick cluster of long setae at the apex and the fringe on the dorsal surface obscure the mandibular teeth when viewed dorsally. The mandibles also bear a number of sensory hairs scattered on them, of which two very long ones are placed ventrally near the apex. The structure and disposition of the various kinds of setae and sensory hairs is shown in Pl. IX, figs. 16 and 17.

Ventrally, the mandible, near its inner lateral border, has a deep cleft, to the distal end of which the retractor muscle is attached.

Maxillae (Pl. IX, figs. 18 and 19). These are situated immediately below and external to the mandibles and are shaped like a mitten, the single-seg-

mented palp representing the thumb. They consist of thin chitin, strengthened by thickenings here and there. Both the dorsal and the ventral surfaces of the maxilla bear numerous strong, simple or branched bristles of various sizes. Among the dorsal bristles of each maxilla, a stout sickle-shaped sensory spine and also a long and much thinner sensory seta arise close together from a small prominence; beside these spines many sensory setae occur scattered on the maxilla, a group of 10 to 12 long hairs arising near the base of the palp.

The *Palp*[1] (*pp*) consists of one segment and, judging from its colour, appears strongly chitinised except distally, where the chitin is very thin. It is cylindrical, gradually tapering distally, its truncated end bearing seven sensory papillae, three large and four small.

Hypopharynx (Pl. IX, figs. 24 and 26). The hypopharynx consists of a soft plate reinforced by rods of strong chitin and lies between the two maxillae, forming the floor of the mouth-opening. Anteriorly it forms the posterior border of the wide slit-like opening (*s.s*) of the salivary or silk glands and is strengthened by a rim of strong chitin. It bears a row of small setae along its length and in the median portion, where the rim is much thicker, it has an extra row of setae arranged like a comb. Along the posterior border of the plate runs a thick chitinous rod curving upwards on both sides. It is slightly enlarged at its upper ends and is connected by means of a fibre of connective tissue to the strong apodeme (*t.t*) proceeding from the anterior border of the epicranial plate.

Labium (Pl. IX, figs. 23–28). The labium lies ventral to the hypopharynx and forms the anterior or ventral border of the salivary slit. At first sight the plate lying immediately below the opening appears to be a part of the hypopharynx and has erroneously been described as such by Johannsen, Pomeroy and others. But on comparing the whole structure (hypopharynx and labium) with that found in the larvae of certain other Diptera, *e.g. Chironomus* (Miall and Hammond, 1892), *Anopheles*, *Culex* (Thompson, 1905, and Howard, 1912), and *Ptychoptera* (de Meijere, 1916) and of some Coleoptera, it seems obvious that the parts lying in front of the salivary opening are portions of the labium shifted backwards. The labium is composed of three parts[2]: (1) a strongly chitinised anterior or dorsal plate, the *Prementum* (*P.m*, Pl. VIII, fig. 1); (2) passing backwards into a soft plate, the *Mentum* (*M*); and (3) a hard, toothed, ventral plate, the *Submentum* (*S.m*).

The *prementum* is a double plate forming the floor of the salivary chamber and bears a pair of broad palp-like structures (*p*) having a number of cup-shaped projections each of which is provided with a two-jointed sensory

[1] Some authors have wrongly described the palps as made up of three segments (Patton and Cragg, 1913), others as of two (Planchon and Verdat). The thinly chitinised distal portion, which at times appears slightly constricted, has probably been mistaken for a separate segment.

[2] I have followed the nomenclature of de Meijere (1916) for the various parts of the labium. Unlike the other larvae described by him, however, in *Simulium* larvae it is the Submentum that is hard and toothed and not the Mentum.

papilla (Pl. IX, fig. 25). Between these two sensory structures there is a pair of strong chitinous spine-like projections on each side of the middle line. The prementum bears a large number of long branching setae along its anterior border and a comb of short stiff ones lying dorsal to the palp-like structures. The ventral wall of the prementum is strengthened by a chitinous thickening on each side and passes backwards into the soft thin *Mentum*. The *Submentum* is the hard chitinous plate[1] lying ventral to the prementum and mentum, and is fused to the head-capsule only along its toothed border. It bears nine strong teeth in the front row (the median tooth and the one at each end much larger than the other six), and a pair of smaller teeth external to the large teeth of the side. Just below these teeth the head-capsule is produced forwards into five broad thin projections (fig. 28). Ventrally, in the region of the submentum, the head-capsule bears on each side 4 to 5 long sensory hairs, some with bifid ends.

The Body.

The body of the larva is somewhat club-shaped, the thorax representing the handle of the club. Its colour is brownish grey on the dorsal surface but becomes much lighter ventrally. Except in the earliest stages the thorax is much swollen, and before pupation, has about twice the diameter of the head. Even in a fairly young larva the three thoracic segments are marked with five pairs of white spots—the histoblasts of the imaginal legs, wings and halters, and with another pair of white spots, which blacken about the middle of the last larval stage, and represent the histoblasts of the nymphal respiratory filaments (Pl. VIII, fig. 5).

The thoracic proleg. The posterior part of the prothorax is produced under the head ventrally into the median thoracic proleg (*C*, Text-fig. 1). It is a truncated conical process with the distal portion jointed and capable of being more or less retracted into the body. At its apex (Pl. IX, fig. 30) the proleg bears radial rows of small hooks by which the larva fixes itself when progressing. Just behind the crown of hooks there is a triangular chitinous plate (*l.p*) lying latero-dorsally on each side, with its anterior border produced into pointed processes arranged in groups of three to five.

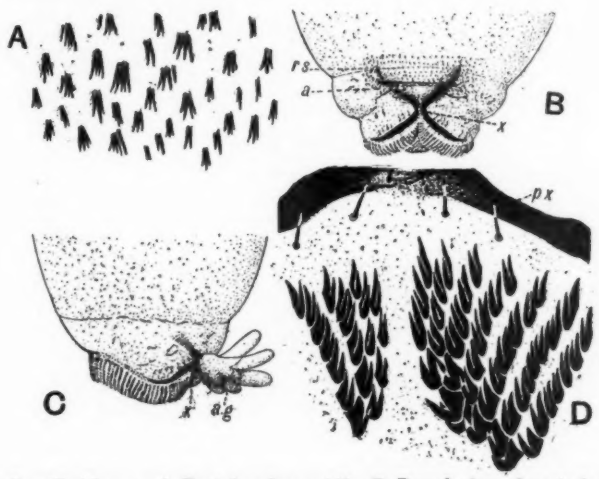
The eight abdominal segments[2] are very faintly marked externally, the greatest circumference being reached in the seventh segment. In the living larva the posterior segments are somewhat flattened ventrally and much arched above. Dorsally on the eighth segment (*B*, Text-fig. 2) lies the median slit-like anus, through which are protruded the three retractile gills, each having 2–4 branches of varying sizes. Posterior to the anal opening is a dark chitinous X-shaped thickening (*x*), the anterior limbs of which end in the region of the anus, while the posterior run for a short distance along the

[1] Wrongly called the "labium" by many writers; some call it the "mentum."

[2] Grünberg (1910), Planchon and others have described the abdomen as composed of nine segments.

border of the posterior sucker. There are a few simple scales lying external to the anterior limbs of the X-shaped sclerite.

The posterior sucker. The end of the abdomen is flattened into a disc-shaped area bearing 70–75 radial rows of strong chitinous hooklets disposed in a circle broken in the medio-dorsal and medio-ventral lines. There are from 8 to 13 hooks in each of the rows except the first three or four on each side of the medio-dorsal line. The hooks are pointed, flattened from side to side and are all directed towards the periphery (*D*, Text-fig. 2).



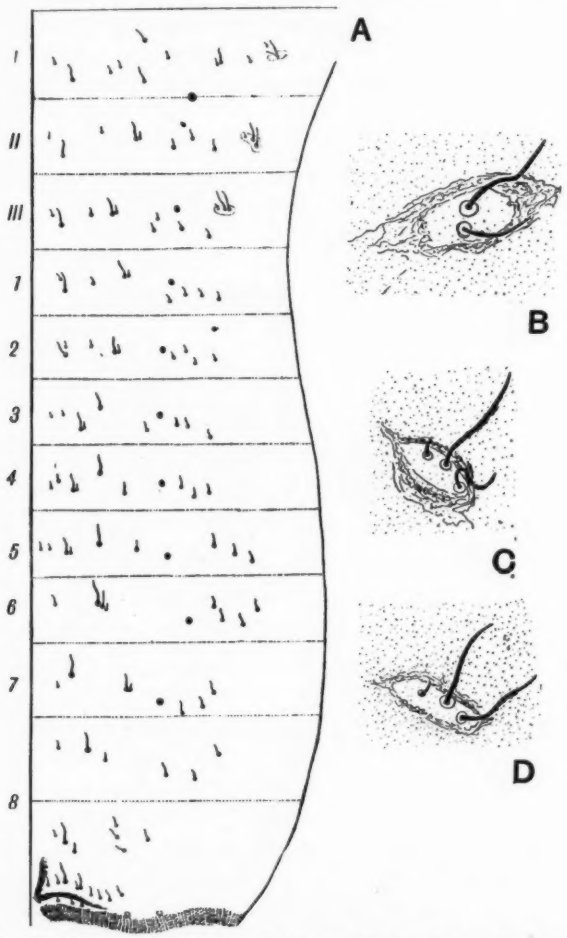
Text-fig. 2. *S. nölleri* larva. *A*, Rectal scales; ×440. *B*, Dorsal view of posterior end; ×42. *C*, Lateral view of posterior end. *D*, A part of posterior sucker near medio-dorsal line; ×440.

a, anus; *a g*, anal gills; *p x*, portion of X-shaped sclerite; *r s*, rectal scales; *x*, X-shaped sclerite.

Most writers have described this posterior appendage as a sucker in the same sense as that found at the posterior end of a leech, but Tonnoir (1923), not finding any muscles inserted in the middle of the disc, says that this organ cannot act as a sucker and that the larva fixes itself only by the help of the hooks. My observations, however, show that there are fairly strong muscles connected with the centre of the disc (Pl. VIII, fig. 10) and that they contract when the larva fixes itself by its posterior end. But in spite of the presence of these muscles the larva cannot fix itself effectively without the further help of the sticky salivary secretion; a fact which may mean that the saliva helps to fill up the spaces between the hooks and thus to form a complete rim all round. There is no doubt, however, that a larva remains fixed to the substratum mainly by means of the hooks which firmly grip the salivary secretion, but it is not possible to say how far the sucking action of the appendage helps the larva at the moment when it first attaches itself to the support. The first-stage larva has a pair of long hairs arising from the middle of the circular area

surrounded by the rows of hooks, and it is therefore very improbable that this appendage functions as a sucker at least in the first-stage larva.

Chaetotaxy (Text-fig. 3). There are numerous very minute sensory hairs scattered irregularly over the dorsal and the lateral surfaces of the body, while



Text-fig. 3. *S. nölleri* larva. *A*, Setal plan of body—medio-dorsal to medio-ventral line. *B*, *C* and *D*, Pleural setae of pro-, meso- and meta-thorax respectively; ×440.

a few longer ones follow a definite arrangement in each of the body segments. The relative size and distribution of the latter may be followed from the diagram *A* (Text-fig. 3).

Each of the three thoracic segments possesses on either side, in addition to the hairs mentioned above, a group of pleural setae, which, according to

Keilin (1915), are the only remains of the thoracic legs of dipterous larvae. In the meso- and meta-thorax each pleural group (*C* and *D*) is composed of three setae, a pair of long flexible ones lying close together, and a solitary short stiff one placed dorsal to the former. In the prothorax, on the other hand, each group has only one pair of long setae lying within an elongated patch (*B*). This seems to be exceptional, since other dipterous larvae have a group of either three or four setae on each side of all three thoracic segments. An examination of the prothoracic group of setae, in the first-stage larva shows, that besides the two long setae, there is a very small conical projection at the dorsal end of the elongated patch. This projection, which represents the third seta of the posterior segments, disappears after the first larval moult.

Internal Anatomy.

Integument.

The integument is composed of a chitinous cuticle and a single uniform layer of flattened hypodermal cells resting on a basal membrane. In the head, the cuticle is strongly chitinised, varying in colour from yellowish-brown to dark-brown, while over the rest of the body it is soft and colourless.

Except in the head a number of large flat cells compose another layer (*Subhypodermal* layer of Viallanes, 1882) in the form of an irregular network immediately beneath the hypodermal cells. These cells have greenish brown or greyish pigment granules[1] distributed evenly in their protoplasm. They make their first appearance here and there 2–3 days after the first larval moult. Cells of a similar nature have been described in larvae of *Musca*, *Eristalis*, *Chironomus* and *Anopheles*. In *Simulium* they are polygonal in outline and form a definite layer beneath the hypodermal cells, each of them containing fat globules of various sizes.

Digestive System.

The wide slit-like mouth lies at the posterior end of a funnel-shaped chamber, which is formed mainly by the overhanging labrum and epipharynx dorsally, and the broad hypopharynx ventrally. The mandibles and the maxillae together form the sides of this chamber.

Foregut. The foregut can only roughly be divided into two regions: (*a*) the *Pharynx* and (*b*) the *Oesophagus*.

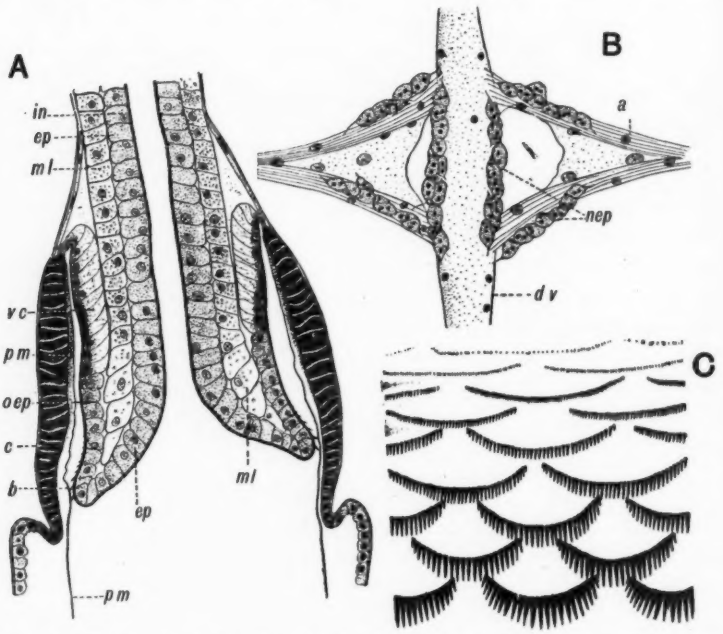
(*a*) The *Pharynx*. The walls of the pharynx consist of a thick chitinous intima, continuous with the general cuticle of the body-wall, and a layer of epithelial cells. Near the anterior end a narrow rib of strong chitin, running from side to side in the ventral wall, divides the pharynx into an anterior and posterior part. In the former both the dorsal and the ventral walls bear many transverse rows of short close-set setae directed backwards and the epithelial lining is distinctly columnar. In the posterior part there is a thick layer of strong circular muscles outside the epithelium and the walls are thrown into three

[1] The colour of these granules varies in the larvae of different species.

longitudinal folds. A number of muscles stretch from the wall of the pharynx to the head-capsule; those in the left half of the head are shown in Pl. VIII, fig. 1, and have been named according to their function and to the place of attachment on the pharyngeal wall.

(*b*) The *Oesophagus*. The pharynx passes gradually into the oesophagus, the walls of which are composed as in the pharynx of the intima (*in*, Text-fig. 4), epithelium (*ep*), circular muscle-cells (*m l*) and thin membrane of connective tissue successively. The lumen is much reduced by three longitudinal folds of its chitinous and epithelial layers.

Oesophageal valve (*A*, Text-fig. 4). The oesophagus gradually widens out as it proceeds backwards and in the prothorax enters the mesenteron. After



Text-fig. 4. *S. nölleri* larva. *A*, Oesophageal valve, longitudinal section. *B*, A portion of dorsal vessel showing alary muscles and nephrocytes. *C*, A portion of chitinous intima of the reflected wall of oesophagus. × 440.

a, alary muscle; *b*, bristles (enlarged in *C*); *c*, wall of cardia; *d v*, dorsal vessel; *ep*, epithelium; *in*, chitinous intima; *m l*, muscle-layer; *nep*, nephrocytes (pericardial cells); *o ep*, reflected epithelium; *p m*, peritrophic membrane; *v c*, vacuolated cells.

continuing for a short distance as an inner tube it is reflected upon itself and passes forwards to meet the mesenteric epithelium, thus forming the *Cardiac* or *Oesophageal valve* (*oe.v*, Pl. VIII, fig. 1). Approaching the anterior end of the valve it forms occasionally a secondary fold. The reflected wall consists only of the chitinous intima and epithelial layer (*o ep*, Text-fig. 4), the muscular

layer[1] of the oesophagus ending at the point of reflection. In the anterior half of the valve the reflected epithelium is greatly modified and has erroneously been described by Miall and Hammond (1900) as a blood space, having a proper wall in the form of a thin membrane and crossed by a number of oblique fibres of connective tissue. The epithelial cells in this region are much enlarged (*v c*) and their contents reduced to only a few strands from a mass of protoplasm lying near the external wall of the cell, where the nucleus usually lies. These cells form a sort of cushion all round the oesophagus. Similar cells have already been described by Pantel (1898) as "*Cellules claires*" in the oesophagus of *Thrixion halidayanum* in the region corresponding to the oesophageal valve of other dipterous larvae. In this case, however, they occur only in the dorsal wall of the oesophagus. Weismann (1864) and Kowalevsky (1887) have described especially enlarged cells, in the oesophageal valve of muscid larvae, but it appears that in *Simulium* they have become still further enlarged. In identically the same position as these cells Van Gehuchten (1890) describes a cavity between the blood-space and the thin epithelial membrane in *Ptychoptera contaminata*. Probably this cavity[2] represents a part of the reflected epithelium which in *Ptychoptera contaminata* shows a further stage of degeneration, and reaches the ultimate stage probably in such forms as *Chironomus* and *Anopheles*.

Anterior to the region of vacuolated cells the epithelial layer decreases in thickness.

The thick chitinous layer of the reflected wall is provided all round in the region of the bend, with a number of festoon-like rows of short stiff bristles (*b* and *C*, Text-fig. 4) pointing backward. Van Gehuchten has also described numerous hooklets covering a part of the reflected wall of the oesophagus in *Ptychoptera* and thinks that their probable function is to enhance secretion in the cells of the cardia, which come in contact with this region. But that the function of these bristles in *Simulium* larvae is to help the passing backwards of the peritrophic membrane, as already suggested by Strickland, seems to be more probable. A slight backward and forward movement of the oesophageal valve within the cardiac chamber is often seen in a living larva but there are no longitudinal muscles in the oesophageal valve or cardia. Possibly the enlarged epithelial cells in the reflected wall or the pair of post-cerebral-oesophageal muscles (*p.oe.m*, Pl. VIII, fig. 1) and the cardiac muscles (*c.m*, Pl. VIII, fig. 2) inserted dorsally upon the oesophagus and cardiac chamber respectively, have something to do with this movement.

[1] Strickland (1913), in his figures of the oesophageal valve, wrongly shows the muscular layer extending only about half-way into the cardiac chamber. In fact, in some sections a double layer of muscle-cells is seen in the apical region of the valve, which leads us to the conclusion that even the muscular layer is reflected to a very small extent. But the cells in this region are much enlarged and vacuolated, with few or no muscle-fibres.

[2] According to Van Gehuchten, this cavity is filled with a finely granulated mass like coagulated blood-plasma but with no blood-corpuscles and the whole is traversed by an irregular network of fine fibrils which disappear on the epithelial membrane externally.

An oesophageal valve seems to be of universal occurrence in dipterous larvae, but its structure varies greatly within the group. Van Gehuchten, in *Ptychoptera*, Miall and Hammond, in *Chironomus*, Saunders (1924), in *Forcipomyia*, and Imms (1907), in *Anopheles* larvae all describe a blood-space of varying size between the oesophageal and the reflected wall near the apex of the valve. The valve of *Simulium* differs from those found in other Nematocerous larvae in that it has no extensive blood space.

Midgut (*M.g*, Pl. VIII, fig. 2). The mesenteron stretches as a straight tube from the prothorax to the seventh abdominal segment, where it meets the hind-gut. It is composed of three parts: (*a*) the *Cardia*, (*b*) the *Mesenteric* or *Gastric Caeca*, and (*c*) the *Stomach*.

(*a*) The *Cardia* (the cardiac chamber of Miall and Hammond, and the *Proventriculus* of other authors) is that portion of the mesenteron which encloses the oesophageal valve. Its walls are composed of a layer of deeply-staining columnar cells (*c*, Text-fig. 4) with large and prominent nuclei and a thin layer of connective tissue on the outside. Proceeding backwards, the cardial walls thin and the cells gradually assume the form of those lining the caeca and the stomach. A pair of broad flat muscular bands, the *cardiac muscles* (*c.m*, Pl. VIII), is inserted in the dorsal wall of the cardia. They have their origin within the dorsal body-wall between the pro- and meso-thorax.

(*b*) The *Mesenteric* or *Gastric Caeca* (*i.c*, Pl. VIII, fig. 2). Just behind the cardia four backwardly directed, somewhat dumb-bell-shaped caeca arise. They are arranged around the midgut as a dorsal and a ventral pair and always appear full of a deep yellow fluid which coagulates in alcohol. Their walls are composed of a layer of large epithelial cells and a thin layer of circular muscles and are enclosed externally by a thin layer of connective tissue. The epithelial cells bulge into the cavity of the caecum and always show a striated margin along the edge of the free border, which appears swollen with a transparent fluid secretion. Between the bases of some of these cells appear solitary globular cells, scattered irregularly and at times appearing like a second small nucleus in the cell.

(*c*) The *Stomach*. The stomach is tubular but slightly dilated in the fifth and sixth abdominal segments. Its walls enclose a peritrophic membrane and consist of the usual layers: epithelial, muscular and connective tissue layers.

The epithelial cells in the anterior part of the stomach are columnar or polygonal, but in the region of the dilatation they are greatly enlarged and bulge considerably into the lumen. (In the latter region they can even be seen as separate cells under a low magnification and in sections stain much deeper than those of the anterior portion.) They give off into the gastric cavity pear-shaped or globular protrusions, which are finely granular and stain very faintly. Similar protrusions in *Ptychoptera contaminata* are considered by Van Gehuchten to be albuminous cell-secretions which burst through a weak spot in the cell-wall as a viscid fluid. Like the cells lining the

gastric pouches, all the epithelial stomach-cells show a markedly striated margin along the free edge directed towards the gut-cavity. (Sometimes similar striations, though not so well developed, are even seen along the free border of the cardial cells.) Under a very high magnification these striations appear to be fine close-set filaments arising from a thin membrane. The striated character of the gastric epithelium is fairly common in Insecta and has been worked out in detail by Van Gehuchten and by Vignon (1901).

Scattered irregularly in the wall of the stomach are isolated globular or pear-shaped cells lying between the bases of the epithelial cells like those found in the cardiac epithelium.

The muscular coat is in the form of a trellis formed of an inner layer of circular muscle-bands and an outer one of longitudinal bands, which lie further apart from one another than the former.

Peritrophic Membrane. The peritrophic membrane lines the whole of the mesenteron except the caeca and completely encloses the food as it passes through the stomach. The membrane consists of a colourless chitin and resists the action of alkalies. Beginning at the anterior end of the cardia, it passes backwards as a tube of a uniform diameter, which is much smaller than that of the stomach. It is free from the wall of the stomach throughout its length, except at its beginning in the cardiac chamber, the space between it and the gastric wall being filled with a yellowish fluid. The membrane is continued beyond the mesenteron into the hind-gut often to a considerable length and at times is even seen protruding from the anus, surrounding the faecal-matter.

Such a chitinous lining of the mid-gut is found in most orders of Insecta, in Myriapoda, some Crustacea and a few Gastropods, and different views are held regarding its origin. Some (like Schneider) hold that it is merely a posterior continuation of the oesophageal chitin, while most authors (like Van Gehuchten and Vignon) believe that it is essentially a secretion of the mesenteric epithelium and is not oesophageal in origin. The recent observations of Chatton (1920) on the peritrophic membranes of Drosophilid larvae and of *Daphnia* (Cladocera, Crustacea) clearly show that there is a diversity in the mode of its formation in the different groups of Arthropoda; he states that in *Drosophila* it is mesenteric in origin, while in *Daphnia* it is a continuation of the oesophageal lining. He also shows, from the study of the behaviour of certain parasites in the alimentary canal of *Drosophila* larva, that the peri trophic membrane is secreted by the cells of the cardia and not by the whole of the mesenteric epithelium. Miall and Hammond (1900) suggest that the copious fluid in the intestinal caeca of *Simulium* may be the peritrophic membrane in the nascent condition, but there is no reason to believe that the mode of its origin in *Simulium* is different from that in *Drosophila*.

Hind-gut. The hind-gut begins in the seventh abdominal segment, and after a short straight course, it forms a small loop on the right side. It is composed of the usual three parts: (*a*) the *Ileum*, (*b*) the *Colon*, and (*c*) the *Rectum*, which can easily be made out externally.

The *Ileum* commences as a small funnel-shaped chamber, where the malpighian tubules enter, and is continued as a tube of uniform diameter. Its walls consist of a thin chitinous intima, an epithelial layer, a layer of circular muscles, and a thin layer of connective tissue on the outside. Just beyond the region of the funnel-shaped chamber, the chitinous layer bears rows of short stiff bristles, like those found on that lining the oesophageal valve. The epithelial layer is very thin and the boundaries of the individual cells are ill defined. The walls of the ileum and the succeeding parts of the hind-gut are thrown into longitudinal folds which involve only the chitinous and the epithelial layers.

Malpighian Tubules (*m.t*, Pl. VIII, fig. 2). The four malpighian tubules open in lateral pairs at the anterior end of the iliac-chamber; the two dorsal ones being longer than the ventral. The tubule cells are filled with greenish-yellow granules (probably excretory substance) and their large nuclei bulge into the lumen of the tube. The portion of the cells which faces the lumen shows a narrow striated margin like that in the cells of the gastric epithelium.

The *Colon* is thick-walled and broader than the ileum. Its walls consist of the same layers as those of the ileum, except that there is no longitudinal muscle-layer which is present in the latter as a poorly developed layer of muscles arranged in narrow bands. The epithelial layer is very much thicker and the cells clearly defined. Unlike that in the ileum, the layer of circular muscles is not continuous but is broken up into broad bands placed at regular intervals.

Posteriorly, at about the middle of the eighth segment the colon passes into the short thin-walled *Rectum* which opens dorsally in a median, slit-like, anus. The epithelial lining of the rectal wall is very thin, the circular muscles poorly developed, and confined to the anterior region. There are no longitudinal muscles. The dorsal wall of the rectum near the anal opening bears irregular rows of branched or simple scales directed backwards (*A*, Text-fig. 2). They are light to dark brown in colour and can easily be seen through the dorsal integument.

From the ventral wall of the rectum, out of a shallow pouch, there arise three branched, retractile processes—the *Anal gills* (*a.g*, Text-fig. 2).

Salivary Glands.

The salivary glands (*S.g*, Pl. VIII, fig. 2) are well developed and lie somewhat ventral to the alimentary canal. They are tubuliform, of varying diameter, and extend backward to the end of the seventh abdominal segment, each gland being doubled upon itself. The glands narrow anteriorly and meet in the prothorax ventrally to the nerve cord. Just anterior to the sub-oesophageal nerve ganglion they pass into a median flattened duct (*S.d*), which opens into a flattened chamber formed between the labium and the hypopharynx. This chamber opens to the exterior by a wide slit (*s.s*) between the anterior end of the hypopharynx and the prementum. The wall of the gland

consists of a single layer of large polygonal epithelial cells which bulge into the lumen of the gland. The cell-nuclei are very prominent and contain a much convoluted chromatin thread and a large central nucleolus. The glands are always filled with a thick sticky fluid which coagulates in water as well as in alcohol. Where the glands meet a short muscle is inserted on the outer side of each gland and is attached to the lateral wall of the body. The median salivary duct has a chitinous lining showing irregular spiral thickenings. Dorsal and ventral muscles control the outer slit-like opening of the salivary chamber. Though the salivary duct and the external opening are single the sticky glandular secretion emerges from the duct in a double stream of flattened threads, applied side by side.

Dorsal or Pharyngeal Glands.

Dorsally to the pharynx, there are a pair of large globular or pear-shaped sessile glands (*d.g*, Pl. VIII, figs. 1 and 2) attached close together to the pharyngeal wall, one on each side of the insertion of the median epipharyngeal muscle. They contain a fluid which coagulates in alcohol. The walls of these glands consist of a single layer of large deeply-staining cells with granular protoplasm, each having a single large nucleus.

These glands appear like a pair of protuberances of the epithelial lining of the epipharynx bulging into the body-cavity; and are attached to the epithelium by means of an extremely short neck. I have not been able to find any opening of these glands either on the outside or into the pharynx. Strickland (1911) refers to these glands as "*Pharyngeal glands*" and says that they secrete a sticky material upon the hairs of the labrum and epipharynx. I have not found any such substance on these hairs, and the glandular secretion does not appear to me to be sticky.

Glands, in the position of the pharyngeal glands of *Simulium* larvae, are uncommon in dipterous larvae; glands in a more or less similar position have so far been described by Keilin (1913) only in a *Mycetophilid* larva (genus *Sciara*) as "*glandes mandibulaires.*" These are probably homologous with the *dorsal glands* of *Simulium*, although *Sciara* possesses an external aperture to the gland which the larva of *Simulium* lacks.

Muscular System.

Muscles of the Head.

The points of attachment of various muscles to the head-capsule correspond to the dark disc-like markings already referred to. Besides the muscles connected with the pharynx, oesophagus and salivary slit, there are a number of strong muscles in the head in connection with the appendages of the head.

Cephalic fans. Each of the fans is provided with a pair of retractor muscles, dorsal and ventral. The dorsal muscle which is much the smaller, arises from the cephalic plate on either side of the medio-dorsal line and is attached to the fan of its side. The ventral muscle, composed of two to three

bands, originates near the posterior border of the cephalic plate and intertwining with that of the other side crosses the head cavity and is attached to a strong apodeme in the fan of the opposite side. When these retractor muscles relax, the fans open out, partly owing to blood pressure and partly to the elasticity of the chitin on the ventral side of the fan. As a rule the fans work alternately with extreme rapidity but at times they may work simultaneously, or again one may close and open a number of times whilst the other rests.

Mandibles. Each mandible is worked by a pair of stout muscles, an outer *abductor* and an inner *adductor*, each composed of four separate bands of muscle fibres arising from the lateral wall of the head. The abductor muscle is attached to the outer hardened edge of the mandible, while the adductor muscle-bands join a strong tendon which enters the mandible, being attached to the distal end of the cleft on its inner side.

Maxillae. Like the mandibles, each maxilla is provided with an abductor and an adductor muscle, the latter being much the stouter. These muscles arise from the lateral wall of the head and are attached to the external and internal wall of the maxilla respectively, the abductor to a ventro-lateral and the adductor to a dorso-lateral point. Consequently the contraction of the adductor muscles bends the maxillae upwards and inwards and as the maxillae are placed ventro-lateral to the mouth opening this movement brings the two together immediately before the mouth. The maxillary palp is provided with a similar but smaller pair of muscles.

Labium. A pair of muscles arises from the ventral wall of the head, one on each side of the thinly-chitinised area and running forwards is attached to the lateral upright projection, the *ascending process* (*a.p*, Pl. IX, figs. 23, 24 and 26) of the prementum. When these muscles contract, the distal end of the prementum with the sensory papillae are moved upwards towards the mouth-opening.

Muscles of the body (Pl. VIII, figs. 6 and 10).

There are well-developed series of dorsal and ventral longitudinal muscles throughout the length of the body. Both the series are segmentally arranged, lying flat against the integument of the larva, the dorsal (tergal) longitudinal muscles lying on each side of the dorsal vessel and the ventral (sternal) muscles, also divided into two similar groups, lying on each side of the nerve cord. There is a pair of oblique tergo-sternal muscles in the three thoracic segments and an inter-segmental, tergo-sternal pair between each two segments of the abdomen. In the prothorax a pair of muscles lies dorsal to the blood vessel and crosses from one group of tergal muscles over to that of the other side. Just behind the prothoracic nerve ganglion there is a transverse muscle stretching from side to side intersegmentally, passing dorsal to the nerve cord. Both the tergal and the sternal muscles of the thoracic proleg pass ventral to this transverse muscle. Besides the muscles mentioned above, there are throughout the body a number of oblique muscles as shown in the figure.

The posterior sucker with its circlet of strong hooks is provided with numerous muscles, originating chiefly in the eighth abdominal segment, though a few are attached to the seventh. Arising from the lateral and the ventral surfaces, they stretch to all points in the circle except the mediodorsal, which is devoid of hooks. A pair of slender muscles arises from the lateral wall of the eighth segment and is inserted upon the middle of the disc. A very stout muscle originating dorsally from the anterior end of the seventh segment, and dividing into two strands, is also attached within this space. The arrangement of these muscles of the posterior appendage is very complicated and can best be followed by reference to Pl. VIII, fig. 10.

Nervous System.

The *Central Nervous System* consists of a *Supra-oesophageal* and a *Sub-oesophageal ganglion* lying in the posterior region of the head, and a chain of eleven ganglia in the body.

The *Supra-oesophageal ganglion* (Pl. VIII, fig. 4), as in other dipterous larvae, is divided into two parts lying dorso-lateral to the oesophagus and linked by a narrow transverse commissure. Latero-anteriorly it gives off, on each side, three nerves: I. A short stout nerve which forks. The inner branch or the *Frontal nerve* (*ar.N*) meets the *Frontal ganglion* (*visceral* system) (*f.g*), while the outer (*F.N*), after supplying the labrum and the lateral wall of the head, subdivides into two, one branch ending abruptly on the integument dorsal to the fans, while the other enters a mass of cells lying at the base of the fans and containing a small ganglion. II. The *Antennary nerve* (*A.N*), which, after giving off a small branch to the head-integument, dorsal to the eyes, immediately forms two branches. The one passes through the imaginal antenna to a small ganglion at the base of the larval antenna into which it sends two fine nerves, one to the two stumpy setae at the end of the second segment and the other to the terminal segment; the other branch ends abruptly on the dorsal integument of the head posterior to the antenna. III. The *Optic nerve* (*op.N*) which runs straight outwards to the eye-spots.

Posteriorly, the supra-oesophageal ganglion, not far from the commissure, gives off a small nerve from each of its lobes; each nerve is connected to the oesophageal ganglion (visceral) (*oe.g*) of its side.

The *Sub-oesophageal ganglion* is somewhat triangular in shape and flattened. Anteriorly it gives off paired nerves to the mouth-parts. The pair of *Mandibular nerves* on each side (*Md.N*, Pl. VIII, fig. 1) run together to the mandibles, one supplying the abductor muscles while the other sends branches to the adductors, enters the mandibles and expands into a small ganglion, giving off small nerves in all directions. The *Maxillary nerve* (*Mx.N*) of each side, near its base, gives off two small lateral branches; one of these supplies the abductor muscle of the maxilla, while the other ends abruptly on the lateral wall of the head. The main nerve gives off a small branch each to the abductor and the adductor muscles and another (which ends in a minute ganglion) to

the base of the maxilla. It terminates near the base of the palp in a small ganglion which supplies fine nerves to the setae and the papillae at the end of the palp. The *Labial nerves* arise close together and send branches to the muscles of the hypopharynx and the labium. Each has at the base of the prementum a small ganglion, which sends small nerves to the two palp-like protuberances.

Nerve Cord. The central nerve cord bears eleven ganglia, three thoracic and eight abdominal. The last three abdominal ganglia are fused together in the sixth segment to form a compound ganglion which shows its three component parts even externally. Each of the eleven ganglia supplies a pair of nerves (which bifurcate near their origin) to their corresponding segments. Of the two branches from the prothoracic ganglion, one goes to the region of the imaginal leg while the other supplies the developing pupal respiratory filaments. In the meso- and meta-thoracic segments, the anterior of the two branches supplies the region of the imaginal wings and the halteres respectively, and the posterior, that of the imaginal legs, the meso-thoracic nerve also sending a small branch to the developing pupal filaments.

The proleg is supplied by a small branch on each side from the nerve of the first thoracic ganglion, which also sends out three fine nerves on each side to supply the neck-muscles.

From the middle portion of the compound sixth abdominal ganglion a pair of nerves runs backwards to supply the seventh abdominal segment. The posterior and largest of the three portions sends out two pairs of long thick nerves, of which the external gives off small branches to the muscles of the eighth segment and the internal pair supplies the muscles of the posterior sucker.

Visceral Nervous System.

There are well-developed *Supra-* and *Infra-intestinal*[1] visceral nervous systems.

Supra-intestinal (Pl. VIII, fig. 4). The frontal nerves (*ar.N*) bend inwards and meet above the pharynx in the long flat triangular *Frontal ganglion* (*f.g*). Before reaching this ganglion they give off small nerves which form a loop anterior to it. The *Recurrent nerve* (*r.N*) runs backwards from the frontal ganglion dorsal to the oesophagus and, just anterior to the transverse commissure, ends in a very minute *Infra-cerebral ganglion* (*i.c.g*). From this ganglion two nerves pass together, ventral to the dorsal vessel, and diverging each joins the *Oesophageal ganglion* of its side (*oe.g*). The *Oesophageal ganglia* lie dorso-lateral to the oesophagus and each is connected to the supra-oesophageal ganglion (*Sp.g*) by a small nerve meeting the latter just behind the transverse commissure. The oesophageal ganglion of each side sends a pair of branches posteriorly. The ventral branch running backwards forms laterally a flat ganglion, the *Post-oesophageal ganglion* (*p.g*), just in front of the cardia.

[1] The nomenclature is that used by Berlese (1909).

This ganglion is somewhat elongated along the margin of the cardia and sends minute branches to the oesophageal valve and to the ventral side of the oesophagus. The dorsal branch from each of the oesophageal ganglia runs backwards on the side of the dorsal vessel and before ending in the *Median ganglion* (*m.g*) near the posterior end of the prothorax, each has a small ganglion, the *Cardiac ganglion* (*c.g*) on the side of the blood vessel. The *Median ganglion* lies dorsal to the blood vessel and sends out on each side a nerve which, bending backwards, is continued alongside the slender suspensory filament (*s.f*, Pl. VIII, fig. 2) from the distal end of the salivary gland. This ganglion is also connected on each side to a diffuse lateral nervous plexus (*n.p*) in the middle of the prothorax.

Infra-intestinal system (Pl. VIII, fig. 2). In connection with each of the thoracic and abdominal ganglia, except the first and the eighth, there is a fine *Transverse nerve* (*t.n*) which lies at the junction between two segments, crossing the nerve cord dorsally. The first of these nerves lies between the pro- and meso-thorax and the last between the sixth and the seventh abdominal segments. Each of these nerves is connected to the ganglion in front (in the thorax) or behind (in the abdomen) by means of a longer or shorter *Median nerve* and an intervening triangular plexus of varying size. Except in the case of the compound abdominal ganglion, these median nerves arise between the double nerve cord from the ventral side of the ganglia near their posterior end, those from the three thoracic being directed backwards, while those from the abdominal ganglia are turned forwards. The median nerves of the last two transverse nerves arise together between the sixth and the seventh abdominal ganglia, that from the sixth bends forwards while the other, the shortest of all, is directed backwards. The sixth and the seventh transverse nerves (running between third and fourth, and fourth and fifth abdominal segments respectively) are connected by a fine longitudinal nerve lying on each side of the nerve cord.

Respiratory System.

The *Tracheal System*[1] (Pl. VIII, fig. 7) consists of a pair of dorso-lateral longitudinal trunks running from the prothorax to the posterior end of the larva. These two main trunks are connected by three dorsal commissures in the thorax, one lying between the pro- and meso-, one in the meso-, and the third in the meta-thorax. These commissures run ventral to the dorsal vessel and send a number of small tracheoles to the dorsal body-wall. Another dorsal commissure, lying between the head and prothorax and running dorsal to the blood vessel, connects the tracheal vessels of the two sides. In each of the segments, from the meta-thoracic to the seventh abdominal, the main trunk sends off ventrally a segmental branch, which near its origin gives off internally a thick bunch of small tracheoles to the alimentary canal. The segmental trachea after a short course divides into a thin ascending branch

[1] It is similar to that described by Taylor (1902) for *Simulium latipes*.

supplying the dorsal body-wall and a thick descending branch which breaks up into a large number of small tracheoles ventrally. Near the origin of the ascending branch, a slender solid tracheole, the *Initial thread*, arises from the segmental trachea. In the seventh segment (abdominal) the initial thread arises from the main trunk[1] instead of from the segmental trachea, which has no ascending branch and supplies only the ventral body-wall of the larva. Each of these initial threads is connected to a closed spiracle (*s*), seen on the lateral wall of the larva as a minute dark-brown chitinous spot[2]. The main trunk sends backwards and inwards a large branch in the seventh abdominal segment to supply the hind-gut and in the eighth segment, after giving off a number of branches on all sides, divides into an ascending and a descending branch both of which ramify profusely to supply the posterior end of the larva. The former sends branches to the anal gills.

At a point where the foremost thoracic commissure arises, the main trunk suddenly bends downwards and after sending a segmental trachea into the mesothorax, again bends forwards. This segmental trachea has no ascending branch but sends a branch backwards to meet a similar branch from the metathoracic segmental trachea, thus forming a loop between the two. An initial thread, which is connected to a large (closed) spiracle belonging to the prothorax[3] is given off from the main trunk close to the root of the mesothoracic segmental trachea. The main trunk, after a short course, divides into two equal branches each of which again divides into two. The lower branch supplies the prothorax and the foot while the uppermost, running dorsally, meets its fellow of the other side to form the anteriormost commissure. The two middle branches supply the head, where they are connected by a small vertical connective.

Simulium larvae, like a number of other aquatic dipterous larvae, are *apneustic* (and not amphi- or peri-pneustic as described by Brauer, 1883, and Grünberg, 1910). Each of the ten pairs of spiracles, one prothoracic, one metathoracic and eight abdominal, is closed by a chitinous plug and is seen as a black speck or scar on the side of the larva.

[1] In the larvae of some species of Simuliidae (such as *S. hirtipes* Fries another, though much finer, initial thread arises from the main trunk in the eighth abdominal segment. Very probably it is present in all the species but is too small to be distinguishable.

[2] The eighth abdominal spiracle is situated on the dorsal surface of the larva but is much smaller than the preceding ones. It is clearly visible, even under a low magnification in the larvae of *S. hirtipes* Fries and *S. ferrugineum* Walb., but in those of other species, it is extremely minute.

[3] Meinert and Grünberg regard this spiracle as belonging to the prothorax, while from its position just behind the tergo-sternal muscle between pro- and meso-thorax, Taylor (1902) concludes that it is mesothoracic. But as the main tracheal trunk passes external to this vertical muscle, no importance can, however, be attached to the relationship of the spiracle to this muscle in the present case. Moreover, by comparison with those other apneustic larvae of eucephalous Diptera in which the tracheal system has been worked out (*Dasyhelea*, according to Keilin, 1921) we find that the most anterior spiracle is pro- and the second meta-thoracic. According to Keilin (1924) the primitive position of Insect spiracles is intersegmental. In Diptera the first pair of spiracles has moved forwards and become prothoracic while all the others have moved backwards, the mesothoracic segment being left without spiracles.

The segmental origin of the tracheal system is marked by the jointed appearance of the main lateral trunk. There are nine such joints to be seen, two in the thorax, and seven in the abdomen, the most anterior being just behind the bend of the lateral trunk. The tracheal system is renewed at every moult and it is at these weak spots that the old lateral trunk snaps, to be withdrawn through the then-open spiracles, at the time of ecdysis.

Anal Gills (*a g*, *C*, Text-fig. 2). There are three anal gills, finger-like, branched or lobed retractile processes, protrusible from the anus. They arise as three hollow projections from the ventral wall of the rectum and when fully extended, curve upwards and forwards towards the head; but when retracted, lie flat on the rectal wall, in a wide shallow pouch. The gill-walls consist of a single layer of large mononucleate epithelial cells supported on a delicate basement membrane and covered externally by thin chitin. The large nucleus of each epithelial cell bulges into the gill-lumen which is continuous with the general body-cavity, and, as seen in sections, it always contains blood. The gills are supplied with fine simple tracheoles. Slender erector muscles and large retractor muscles, both paired, are connected with the gills. There are no muscles to protrude the gills and it appears that this is accomplished by the flow of blood under pressure of the muscles of the body-wall.

Osten-Sacken (1870), Townsend (1895) and others regard the anal gills as purely tracheal gills, while Miall and Hammond, and Johannsen consider them to be only blood gills (without trachea). But the presence of both blood and tracheae[1] in the cavity, obviously leads to the conclusion reached by Headlea (1906) that the gills of *Simulium* serve both as blood and tracheal gills.

The whole larval body-wall is richly supplied with small tracheoles, which doubtless assist the gills in respiration. Although *Simulium* larvae have closed spiracles, they live much longer in a moist atmosphere (*e.g.* wrapped up in a damp cloth) than in stagnant water. When larvae are kept damp, the anal gills are completely retracted and respiration obviously takes place through the body-wall.

Reproductive System.

The rudiments of the gonads, as seen in the last stage larva, lie dorsally along the body-wall, one on each side of the dorsal vessel; they differ in form in the two sexes, being longer in the female than in the male. In the *Female* (Pl. VIII, fig. 9), the gonad is divisible into two parts, a posterior thick fusiform *Generative region* (*gn*) lying in the sixth abdominal segment and an anterior filiform portion, the *Terminal filament* (*g.f*) which traverses the fat-body, following the lateral tracheal trunk, as far as the second or third

[1] The number of tracheoles in the gills of the larvae of *Simulium nölleri* and other British species is not very large, but in the larvae of *S. damnosum* and even of *S. reptans*, found in the tropics, the gills are supplied, according to Roubaud (1906 and 1907), with large tracheae which branch profusely in the walls of the gills.

abdominal segment. The generative region consists of clusters of large rounded cells, the oocytes, separated by transverse partitions of smaller cells, the interstitial tissue. The developing oviduct (*g.d*) arises from the posterior end of the generative region and, running backwards along the body-wall, ends near the median ventral line about the middle of the eighth segment, a little in front of a median imaginal disc (*i.g*). In the *Male* (Pl. VIII, fig. 8) the rudiment is very short, globular or pear-shaped and also lies in the sixth abdominal segment. The *Anterior filament* is extremely fine and does not extend beyond the fifth segment. The *Generative region* (*gn*) consists of many irregularly distributed clusters of small cells, the *Spermatocytes*. Unlike the future oviducts, the developing male genital ducts (*g.d*) end laterally near the posterior end of the larva, in the region of an imaginal disc (*i.g*) on each side. There is no median ventral imaginal disc in the eighth segment in the case of the larva which is to develop into a male fly.

Circulatory System.

The dorsal vessel is flattened dorso-ventrally and stretches from the seventh abdominal segment to the head, where it ends in the region of the brain. The posterior portion of this vessel, lying in the seventh abdominal segment, is slightly dilated to form the *heart* (*ht*, Pl. VIII, fig. 2) and is provided with two pairs of *ostia* (*os*, Pl. VIII, fig. 3). The terminal pair divides the "heart" into two chambers, the posterior very small and globular, the anterior large with subparallel sides. The second pair of ostia marks the anterior end of the heart.

The ostia are elliptical in shape and are placed latero-ventrally in the wall of the heart. In a living larva the borders of the ostia show faint radiating lines. As in other dipterous larvae, each ostium is guarded by a pair of enlarged cells (*v*) which surround the opening and are noticeable by their bulging nuclei even in living specimens.

The heart-wall consists of flattened muscle-cells, the striated muscle fibres being arranged in transverse rows (*m.h*), except in the wall of the small terminal chamber. These rows of fibres are best seen at the sides of the heart, since they fade away both dorsally and ventrally, leaving a clear space in the median line. The cell-nuclei (*n*) are easily seen on each side bulging slightly into the heart-lumen, and are neither arranged opposite one another in pairs (as in *Chironomus*, *Culex* and *Notonecta* according to Jaworowski, 1880), nor alternately (as in *Corethra*) but follow no definite arrangement.

Ventral to the heart lies a loose fibrous network, the *Pericardial septum* (*p.s*), whose fibres are connected to the ventral heart-wall; a few strong fibres which arise from the posterior end of the heart giving support to that region.

The blood vessel in front of the heart is divisible into two parts: (1) a long *Intermediate region* extending as far as the beginning of the abdomen, and (2) a slightly narrower anterior region, the *Aorta*. There are no *inter-ventricular valves* (Jaworowski) or "valves" (Popovici-Baznosanu, 1905) as found in some *Chironomus* larvae marking the passage of the heart into the *intermediate*

region. In the *intermediate region* the vessel-wall resembles that of the heart except that the muscle fibres, which gradually become longitudinal anteriorly, are very much fainter and there are not even rudimentary ostia. The intermediate region is supported by seven pairs of *alary muscles* which are inserted into its ventro-lateral surface without splitting into dorsal and ventral bands, as they do in *Anopheles* (Imms) and *Thrixion* (Pantel). These muscles are markedly striated and follow the same arrangement as in the majority of Nematocerous larvae (*e.g. Chironomus*).

The *Aorta* opens into the body-cavity by means of a wide slit-like opening, just behind the dorsal brain-commissure. The dorsal border of the opening is attached to the dorsal commissure, while the ventral border lies free on the oesophagus. In the thorax the aorta is attached to the body-wall by means of fine intersegmental fibres which do not seem to be muscular.

An elongated compact mass of uninuclear cells (*m.c*, Pl. VIII, fig. 4) lies in the anterior region of the thorax along each side of the dorsal vessel. The cells are slightly vacuolated and appear much like small fat-body cells. In *Anopheles maculipennis*, Imms (1908) has described a pair of similar masses of cells (but multinuclear) which he thinks are probably nephrocytic[1] in nature. According to him there is another mass of vacuolated cells (uninuclear) lying ventral to the blood vessel in the brain-region and this he has compared to the *Anneau de Soutien* of Pantel or the "Weismann's Ring." Frew (1923) describes a mass of similar cells in *Forcipomyia piceus* as "Weismann's Ring" lying on the dorsal vessel in the prothorax, but according to Saunders (1924) in *F. bipunctata*, the anterior half of this mass is nephrocytic in function (*v. infra*). Unlike that in the larvae of *Anopheles maculipennis*, in *Simulium* larvae there is no mass of cells in relation to the anterior opening of the blood vessel where the *Anneau de Soutien* of Pantel or the *Anneau Péricardial* of Keilin, is always found in Cyclorrhaphous larvae. It is difficult to say how far the mass of vacuolated cells lying in the prothoracic region of *Simulium* larvae is comparable to the *Anneau Péricardial* (or "Weismann's Ring") of Cyclorrhaphous larvae, but it seems probable that it is homologous to the mass found in the thoracic region of *Anopheles*, *Forcipomyia* and *Corethra* (according to Dogiel, 1877) and there is no doubt that it is not nephrocytic in function.

Nephrocytes.

The nephrocytes[2] of *Simulium*, like those of Cyclorrhaphous larvae (Keilin, 1917) can be separated into two groups according to their position: (1) Peri-oesophageal or ventral nephrocytes and (2) peri-cardial cells or dorsal nephrocytes.

[1] By feeding larvae of *Anopheles plumbeus* on carmine granules, I find that this mass is not nephrocytic in function for it does not take up the carmine though the true nephrocytes become fully charged therewith.

[2] The distribution of nephrocytes was studied by feeding the larva on carmine granules.

The *Peri-oesophageal nephrocytes* lie ventro-laterally to the oesophagus, behind the brain, in the form of a loose chain of 6–8 cells on each side. The chains are attached anteriorly by a fine connective filament to the visceral nervous plexus (*n.p*, Pl. VIII, fig. 4). The nephrocytes are somewhat spindle-shaped, the finely filamentous ends of neighbouring elements being interconnected. Each nephrocyte contains two large nuclei with a sharply marked nucleolus in each. Living nephrocytes are yellowish-green in colour and their protoplasm is full of numerous droplets of various sizes.

The *Pericardial cells* (*nep*, Text-fig. 4, *B*) are arranged in seven pairs of groups in the form of small chains placed inter-segmentally in the abdomen on either side of the dorsal vessel and spreading along the alary muscles. The pair of groups lying at the anterior end of the first abdominal segment (in front of the single alary muscle) is only about half the size of those in the succeeding segments. The number of cells in the various groups increases gradually as they proceed backwards. In some specimens a few pericardial cells are seen attached to the fibrous network at the posterior end of the heart.

Besides the pericardial cells in the abdomen, a chain of nine to fifteen nephrocytic cells lies in the prothorax on each side of the dorsal vessel.

The pericardial cells are attached to the dorsal vessel and to one another by means of fine connective filaments and in structure are like the peri-oesophageal nephrocytes. In the abdomen some of the pericardial cells are sometimes much smaller (about $\frac{1}{3}$) than the others in the same group, but these smaller nephrocytes are also binucleated.

By feeding and injecting larvae of the various families of Nematocerous Diptera with carmine[1], I find that the two groups, Peri-oesophageal[2] and Pericardial nephrocytes, are of almost universal occurrence, the only exception being *Forcipomyia*, in which, according to Saunders, the peri-oesophageal group of nephrocytes is absent. However, the number and distribution of the nephrocytes (especially the pericardial) in the larvae of each of the families is not so constant as it is in Cyclorrhaphous larvae.

The additional group of nephrocytes occurring in the prothoracic region of *Simulium* larvae (*v. supra*) is exceptional and has so far been found only in *Forcipomyia*, in which there is a median mass lying above the dorsal vessel in the same region.

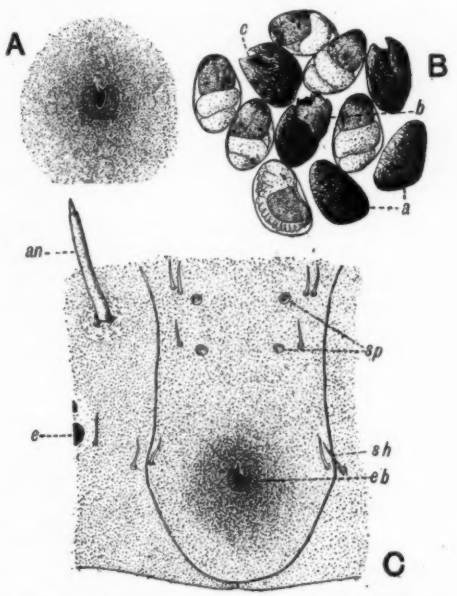
(B) The First-Stage Larva.

The first-stage larva is from 0·6 to 0·9 mm. long, without any pigmentation on the body and is easily recognisable from those of the other stages by the presence of a black spot dorsally on the head. The head is comparatively large and, except for the black spot, is of a more or less uniform grey colour. It has the same shape as that of the fully-grown larva excepting

[1] For methods see Kowalevsky (1889) and Nuttall and Keilin (1921).

[2] Miall and Hammond (in *Chironomus*), Bruntz (1904) (except in *Culex*) and Imms (in *Anopheles*) do not mention anything about the Peri-oesophageal nephrocytes.

that the epicranial plates meet dorsally behind the clypeus (*C*, Text-fig. 5). Between the four groups of discs (which are extremely faint) in the middle of the clypeus is situated a small black tooth-like projection, the *Egg-burster* (*A*, Text-fig. 5), which is slightly curved anteriorly. Around the tooth the pigment spreads on all sides and the whole structure appears as a conspicuous black spot on the head (*e b*, Text-fig. 5). According to Edwards (1919) the egg-burster is found in several eucephalous dipterous larvae of different families. In *Simulium* larvae, instead of the light-coloured membranous area around the central tooth found, for example, in *Culicidae*, there



Text-fig. 5. *S. nölleri* first-stage larva. *A*, Egg-burster. *B*, Cluster of eggs; ×42. *C*, Portion of head-capsule; ×440.

a, unhatched eggs; *an*, antenna; *b*, larva hatching out; *c*, empty egg-shell; *e*, eye-spots; *e b*, egg-burster; *s h*, sensory hair; *s p*, sensory pit.

is a dark plate on each side which from its colour appears to be strongly chitinised (*A*, Text-fig. 5). The sensory pits and the various sensory hairs are present in their usual places, the latter comparatively much longer than those in the later larval stages[1], but the microsetae are all absent. I have failed to find on the side of the egg-burster the extra hairs which, according to Edwards (1921), disappear after the first moult. Each Antenna (*an*, Text-fig. 5) is only

[1] The presence in younger larvae of relatively longer setae than in full-grown specimens has already been observed in *Bibio* (Morris, 1921), *Forcipomyia* (Saunders), *Cyclorrhapha* (Keilin, 1911, 1915) and appears to be of very common occurrence.

two-segmented[1] with a pair of small stumpy projections lying near its base. The cephalic fans bear but twenty filaments each with a few stout setae. On each of the mandibles the rows of teeth, proximal to the three terminal black teeth, are represented only by four pointed bristle-like projections and there is only a rounded process on the inner edge instead of the two flat tooth-like projections found in the later stages. The two palp-like processes on the prementum are comparatively large and each has five finger-like papillae, like those at the end of the maxillary palp. The submentum has the usual nine teeth in the front row but the median tooth is very much elongated, and ventrally there is only a single hair on each side. There are very few hooks on the thoracic proleg. The hooks on the posterior sucker are arranged in three concentric rows and in the middle of this circlet there is a pair of long hairs which disappears after the first moult. The three gills are simple and there is only a slight protuberance at each of their bases which indicates the branching nature of the gills in later stages. There are no other lobe-like branches at the posterior end as described by Barnard (1880), which, according to him, disappear in the later stages of larval development. Contrary to Strickland, I find that this larva uses its cephalic fans in feeding like the older larvae. In a first stage larva, 10 to 12 hours old, the *peritrophic membrane* extends back only about half the length of the stomach and is at times very much wrinkled near the posterior end of the oesophageal valve. The nerve cord shows eleven somewhat separated ganglia, and the tracheal system contains no air.

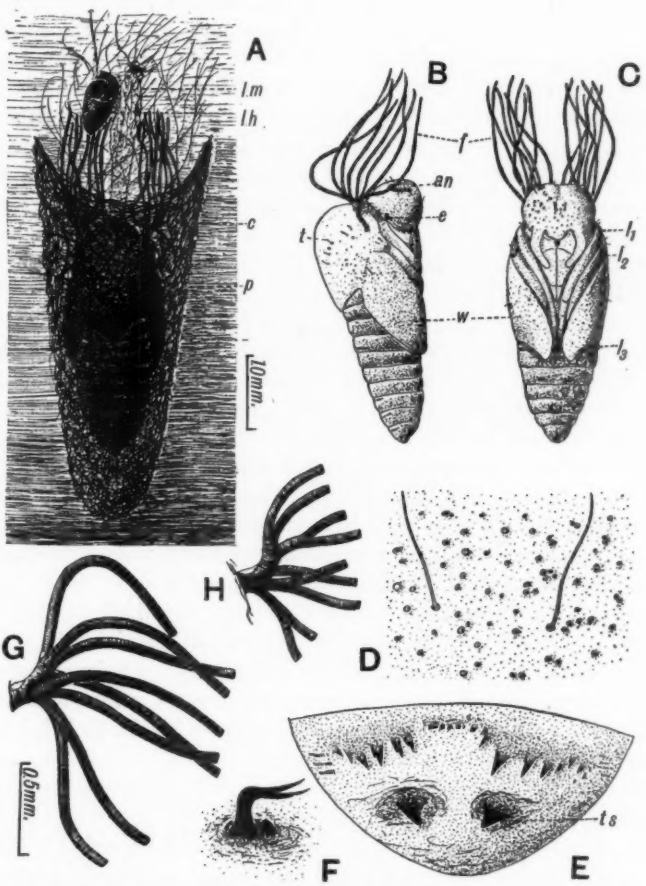
(C) The Pupa.

Pupae of *Simulium nölleri* very often occur in large clusters, sometimes in two or three superposed layers. The pupa lies almost completely within the cocoon and when taken out measures about 3·9 mm. in length (without the filaments) and about 1·4 mm. in breadth (in the thoracic region). The pupal head is small, somewhat folded on the thorax ventrally, and has a pair of pigment spots on each side. These are the remains of the larval eyes which have been described in other eucephalous Diptera (*Belgica antarctica*, by Keilin, 1913) and which probably persist beneath the eyes of the imago. The thorax is very convex, with pro- and meso-notum fused and meta-notum in the form of two small triangular plates, one on each side of the conical scutellar process of the meta-notum. Dorsally the head and thorax are covered with many minute disc-like tubercles of a darker colour than the cuticle of the body (*D*, Text-fig. 6). These tubercles, which are of solid chitin, are of different sizes

[1] The growth of the antenna in *Simulium* larvae is rather unusual among Insects, as the increase in the number of segments takes place by addition in the first two larval stages and by intercalation after the second-stage larva.

From the presence of the pair of stumpy projections at the base of the antenna (*C*, Text-fig. 5), it is obvious that this two-segmented antenna represents the two terminal segments (Pl. IX, fig. 15) of the antenna of a full-grown larva. In the second-stage larva (to be dealt with later) a third segment is added to the antenna from below, while in the third stage a fourth segment has been intercalated between the basal and the second segment of the antenna of the second stage larva.

in the various species and lie much closer together in some than in others. The abdomen, viewed dorsally, shows nine clearly-marked segments, whereas, viewed ventrally, the three anterior segments are covered by the wing and leg sheaths (*A–C*, Text-fig. 6).



Text-fig. 6. *S. nölleri* pupa. *A*, Pupa *in situ* within the cocoon. *B*, Lateral view of pupa. *C*, ventral view of pupa. *D*, Portion of thoracic wall showing tubercles and "trichomes." *E*, Dorsal view of terminal segment. *F*, Ventral spine from segment 4. *G*, Respiratory filaments of right side (ends amputated). *H*, Filaments of a variant (ends of filaments amputated).

an, antenna; *c*, cocoon; *e*, remains of larval eyes; *f*, filaments; l_1–l_3, legs; *l.h*, moulted larval head-capsule; *l m*, larval moult; *p*, pupa; *t*, trichomes; *t s*, terminal spines (or hooks).

The head bears three pairs of simple sensory hairs and there are five pairs dorsally and six laterally on the thorax (pro- and meso-notum). The dorsal thoracic hairs are placed in two groups (two in one and three in the other),

with a sensory pit near each group (*t*). These hairs (*D*, Text-fig. 6) or *trichomes* of Lutz (1913) differ in length in various British species, being branched in one. Near the base of the respiratory filaments there is another group of six short stiff sensory hairs. Dorsally on the abdomen there is a row of six sensory hairs on each side of the second segment, and on the third and fourth, near their posterior border, are four strong cuticular hooks on each side, pointing forwards, but individual variations in the number of these hooks are fairly common. On each of the seventh, eighth and ninth segments, there is a row of backwardly-directed cuticular spines along the anterior border. The number of spines in these rows is variable but in some species the rows are much better developed than in others and are also present in other segments besides the last three. The ninth segment bears near its posterior end a pair of backwardly-directed *terminal spines* or *hooks* (*t s*, Text-fig. 6, *E*), the size of which varies in the different species. On the ventral surface the fourth abdominal segment bears on either side a strong cuticular spine bent forwards (*F*, Text-fig. 6), and a pair of similar spines lie close together, on the fifth, and a pair, rather further apart, on each of the sixth and seventh segments. These spines are bifid but occasionally they may be simple. The ventral spines on the fourth segment are absent in some British species, while in others they are very small, but in all species those on the fifth, sixth and seventh segments are constant in number as well as in position.

Respiratory Filaments[1] (*G*, Text-fig. 6). The respiratory filaments are about as long as the pupa. They are eight in number on each side, the only exception (out of a very large number of pupae examined) was a male pupa[2] which had nine filaments on each side (*H*, Text-fig. 6). The filaments arise on each side from the region of the prothorax, by a common stalk, which gives off near its base four filaments in two shortly-stalked pairs. The remaining four filaments placed near the distal end of the stalk are not arranged in pairs and are widely divergent near their base. Three of them arise from a common base or a very short common stalk, while the fourth originates by itself a little below them. The uppermost filament is nearly vertical for some distance from its origin. The filaments are transversely wrinkled and their surface is roughened by extremely minute protuberances. The number of filaments and the mode of branching are constant for every species, but when the number is very large (more than ten) there may be slight individual variations. According to Pomeroy (1922) in some of the African species the mode of branching is very variable but the appearance and structure of the chitinous wall of the filaments seem to be constant. In British species the mode of branching is very constant

[1] *Respiratory filaments* of pupae of *Simulium* are homologous to the "*Prothorakalhorns*" (de Meijere, 1902) of pupae of various other Diptera and have been described as *tracheal gills* by many writers. On account of the complete absence of tracheae in these filaments of *Simulium*, Volger (1887) called them *Röhren Kiemen* (tube-gills) and Taylor (1902), who has described the tracheal system of *Simulium* in detail, has given them the name of *Cuticular Gills*.

[2] At my request Mr F. W. Edwards dissected out the genitalia of this specimen and found them to be like those of a typical *S. nölleri*.

and I have failed to find any characteristic difference in the appearance of the outer cuticle of the filaments except in the case of *S. equinum*, which however can easily be recognised by other characters.

The *Cocoon* (*c*, Text-fig. 6, *A*) has a golden or yellowish-brown colour and is of the form of a wall-pocket, narrowing posteriorly towards its rounded bottom. The anterior portion of the cocoon is very loosely woven and there are many window-like spaces in the web. The floor of the cocoon is very thin and is absent in the anterior one-third. The spines on the ventral side of the pupa are entangled in a number of fine silk threads arising from the posterior end of the floor, while the hooks on the dorsal surface are fixed in the dorsal wall of the cocoon. The structure and the shape of the cocoon is fairly constant and serves as a very useful distinguishing character for certain species.

Material Collected. I have found the early stages of this species in very large numbers in the River Cam, near Hauxton, as well as at Cambridge, and in the River Lark near Barton Mills (Suffolk). A single pupa occurring in company with the pupae of *S. aureum* Fries was obtained by M. Séguey (Paris Museum) from the River Yonner near Sens, France.

EXPLANATION OF PLATES VIII AND IX.

(All figures refer to the larva of *S. nölleri* Fried.)

PLATE VIII.

Fig. 1. Lateral optical section of the head and first two thoracic segments of larva.

Fig. 2. General dissection of the internal anatomy viewed from the right side. The dorsal wall of the larva with the blood vessel is displaced to the left. The right half of the head-capsule has been cut away.

Fig. 3. Ventral view of the heart, also showing the pericardial network. ×152.

Fig. 4. Dorsal view of anterior portion of alimentary canal showing the supra-intestinal visceral nervous system.

Fig. 5. Lateral view of fully-grown larva, showing the imaginal discs and the developing pupal respiratory filaments.

Fig. 6. Left half of the larva showing the muscular system of the body. (Head has not been dissected out.)

Fig. 7. Lateral view of the tracheal system of the larva (from the left side).

Fig. 8. Posterior portion of the larva showing the developing female genital organs.

Fig. 9. Posterior portion of the larva showing the developing male genital organs.

Fig. 10. Posterior end of the larva showing the muscles in relation to the posterior-sucker.

PLATE IX.

Fig. 11. Dorsal view of cephalic fan (opened out) of the left side. ×42.

Fig. 12. Ventral view of cephalic fan (opened out).

Fig. 13. A filament from the cephalic fan. ×100.

Fig. 14. Antenna of the right side. ×152.

Fig. 15. Distal end of the antenna. ×440.

Fig. 16. Dorsal view of the left mandible.

Fig. 17. Ventral view of the left mandible.

Fig. 18. Ventral view of the left maxilla.

Fig. 19. Dorsal view of the left maxilla.

Fig. 20. Distal portion of the right mandibles (long bristles on the dorsal side of the mandibles have been removed). ×440.

Fig. 21. Ventral view of the labrum.

Fig. 22. Dorsal view of the labrum.
Fig. 23. Ventral view of the prementum; also showing the portion of the salivary duct where it opens into the salivary chamber.
Fig. 24. Lateral view of the hypopharynx and the prementum.
Fig. 25. Portion of the prementum showing the palp-like structures. × 440.
Fig. 26. Dorsal view of the hypopharynx and the prementum.
Fig. 27. Ventral view of the submentum.
Fig. 28. Distal end of the submentum. × 440.
Fig. 29. End of the labrum, after removing all the long bristles.
Fig. 30. Lateral view of the thoracic proleg.

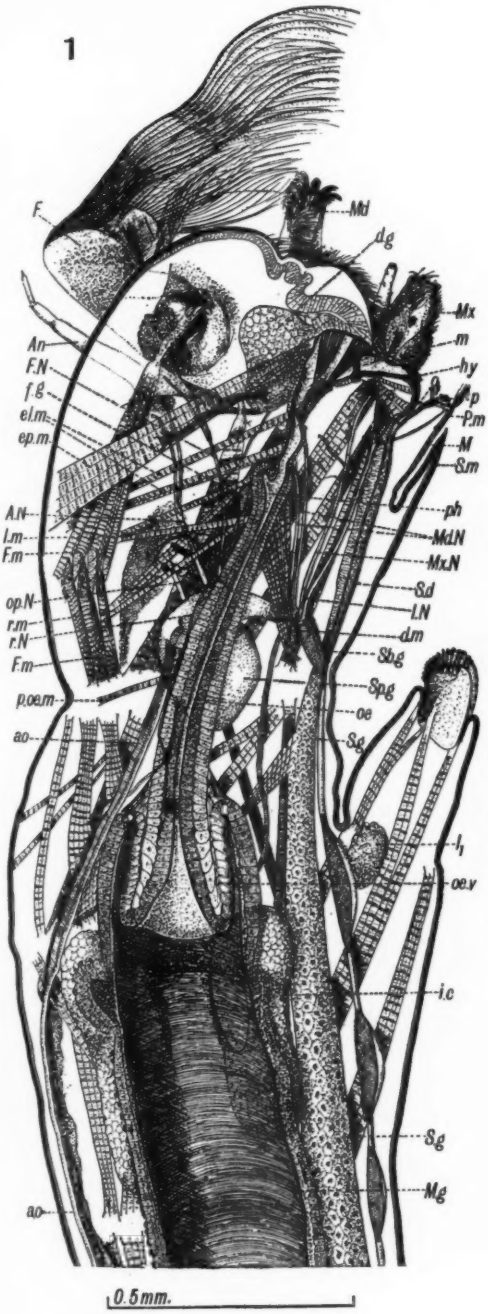
(Fig. 16–19, 21–24, 26, 27, 29 and 30 have the same scale as Fig. 14.)

KEY TO LETTERING OF PLATES.

a.g	Anal gills.
a.m	Alary muscle.
An	Antenna.
A.N	Antennary nerve.
ao	Aorta.
a.p	Ascending process of prementum.
ar	Place of articulation of prementum and hypopharynx.
ar.N	Frontal nerve.
b	Bush-like cluster of bristles.
b.t	Bristle-like teeth.
c.c	Cardiac chamber.
c.g	Cardiac ganglion.
c.m	Cardiac muscle.
d.g	Dorsal gland.
d.m	Dilator oesophageal muscle.
e	Eye spot.
el.m	Elevator muscles.
ep.m	Epipharyngeal muscle.
F	Cephalic fan.
f	Developing pupal-respiratory filaments.
F.f	Filaments of the fan.
f.g	Frontal ganglion.
F.m	Muscles of the fan.
F.N	Nerve of the fan.
g.d	Developing genital duct.
g.f	Developing genital filament.
g.h	Group of hooklets.
gn	Developing gonad.
h	Imaginal-disc of halter.
H.g	Hind gut.
ht	Heart.
hy	Hypopharynx.
i.c	Mesenteric or gastric caeca.
ic.g	Infra-cerebral ganglion.
i.g	Imaginal disc of genitalia.
i.p	Internal process of the prementum.
l_1, l_2, l_3	Imaginal discs of the 1st, 2nd and 3rd legs.
l.m	Lateral pharyngeal muscle.
l.N	Labial nerve.
l.p.	Lateral plate on proleg.
M	Mentum.
m	Mouth-opening.
m.c	Mass of cells along the aorta.
Md	Mandible.
Md.N	Mandibular nerves.
M.g	Mid-gut.
m.g	Median ganglion.
m.h	Muscles of the heart.
mt	Malpighian tubules.
Mx	Maxilla.
mx	(Mx).
Mx.N	Maxillary nerve.
n	Nucleus.
ne	Nephrocytes.
n.p	Nerve plexus.
o	Opening of the salivary duct.
oa	(*ao*).
oe	Oesophagus.
oe.g	Oesophageal ganglion.
oe.v	Oesophageal valve.
op.N	Optic nerve.
os	Ostea.
p	Palp of prementum.
p.g	Post oesophageal ganglion.
ph	Pharynx.
P.m	Prementum.
p.oe.m	Post-cerebral oesophageal muscle.
pp	Maxillary palp.
p.s	Pericardial septum
r.m	Retractor pharyngeal muscles.
r.N	Recurrent nerve.
s	Spiracular scar.
Sb.g	Sub-oesophageal ganglion.
S.d	Salivary duct.
s.f	Suspensory filament.
S.g	Salivary gland.
S.m	Submentum.
S.o	Region where salivary duct opens into salivary chamber.
s.p	Sensory process.
Sp.g	Supra-oesophageal ganglion.
s.s	Salivary slit.
s.t	Row of three light-coloured teeth.
t	Terminal teeth (black).
tn	Transverse nerve.
t.p	Tooth-like process.
tr	Tracheal trunk.
t.t	Inner end of the tentorial process.
v	Valve of the ostea.
w	Imaginal disc of the wing.

To be continued in our next number.

(*MS. received for publication* 20. v. 1925.—Ed.)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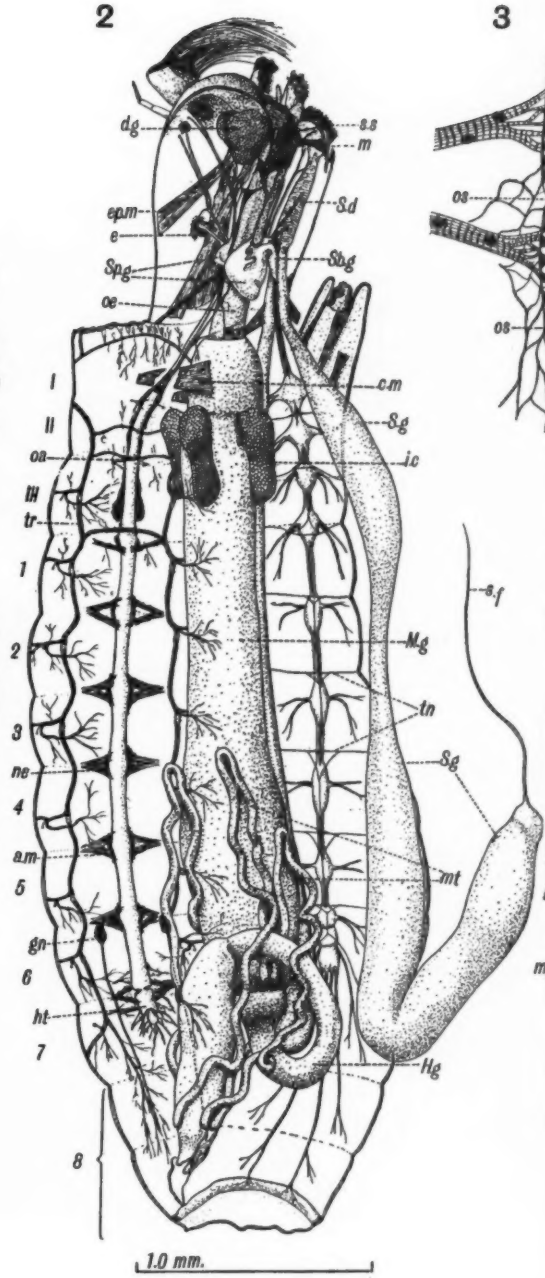
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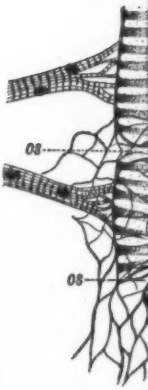
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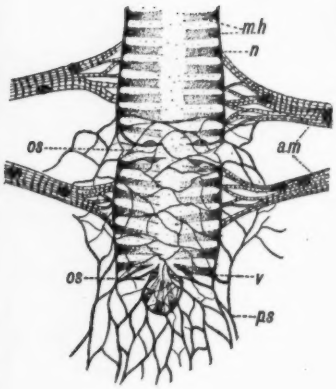
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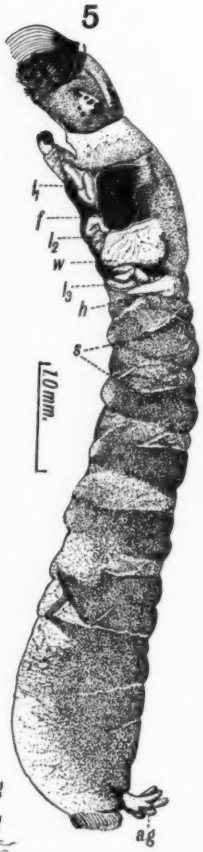
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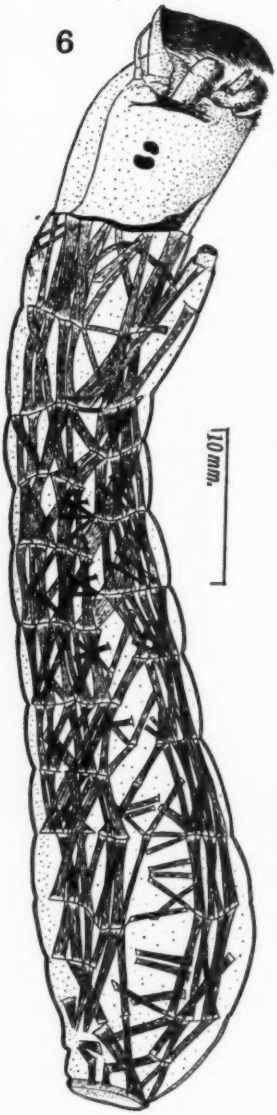
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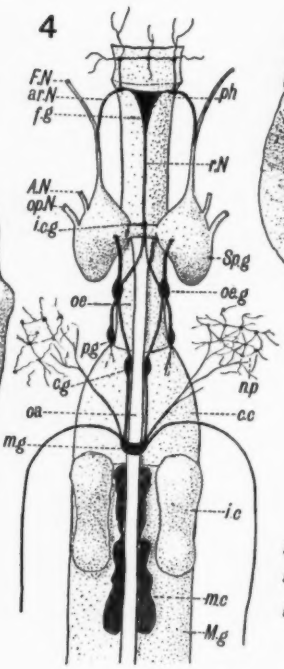
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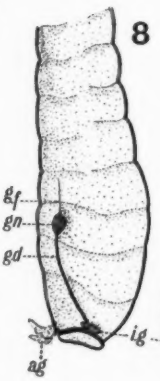
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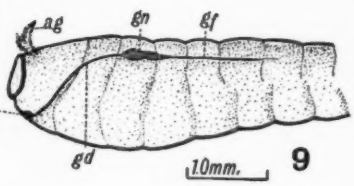
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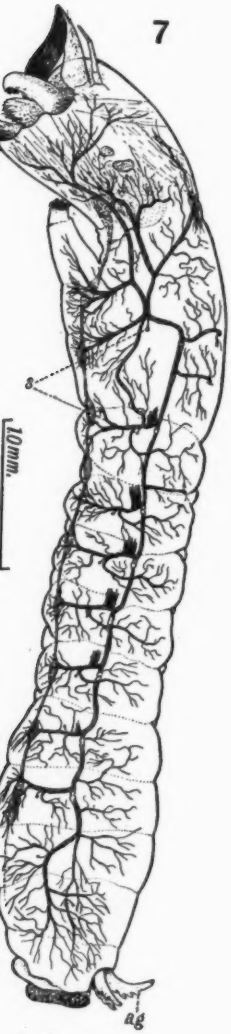
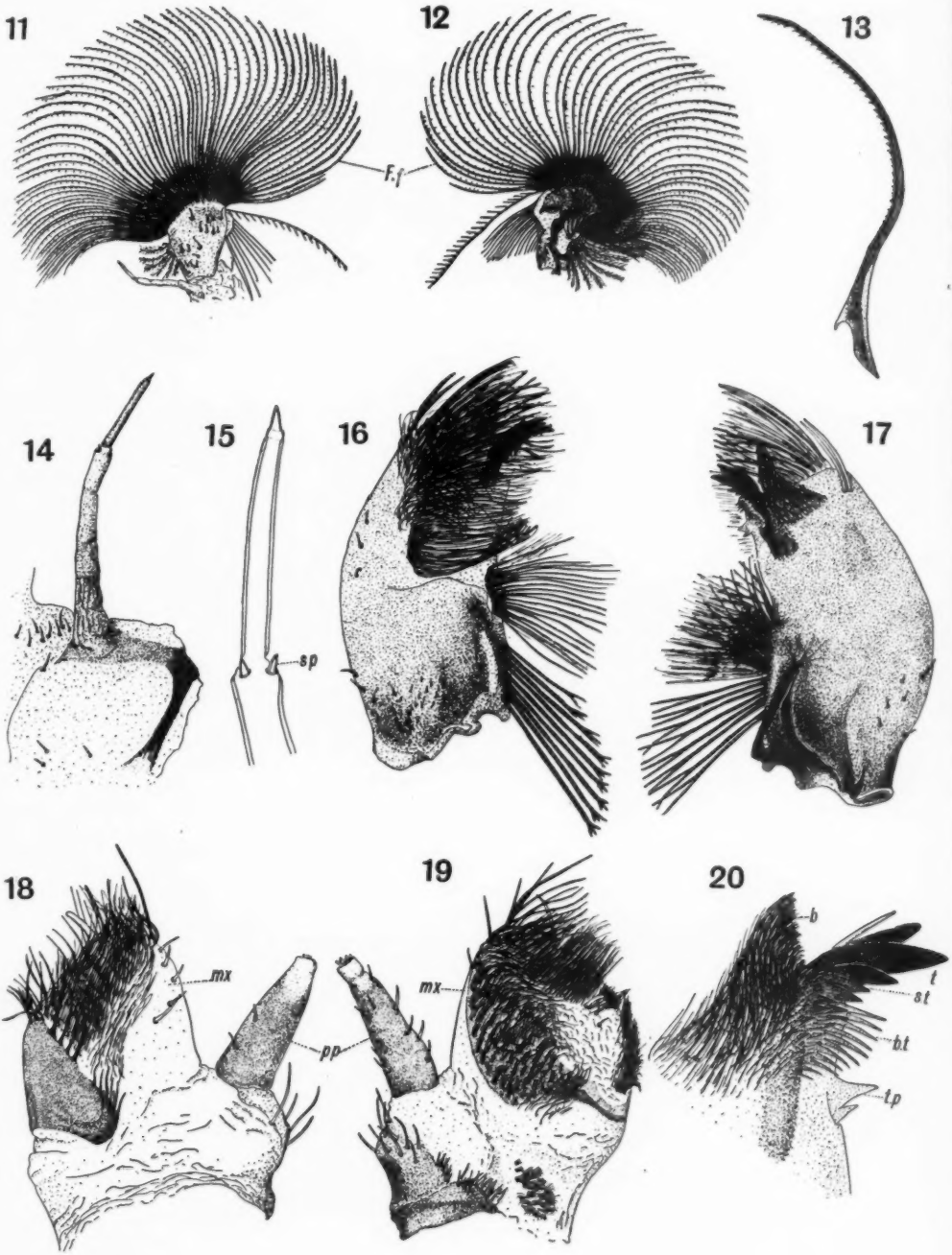
PLATE VIII





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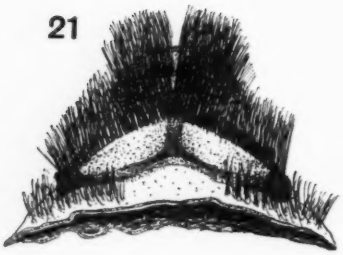

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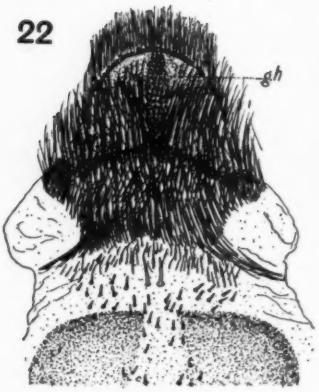

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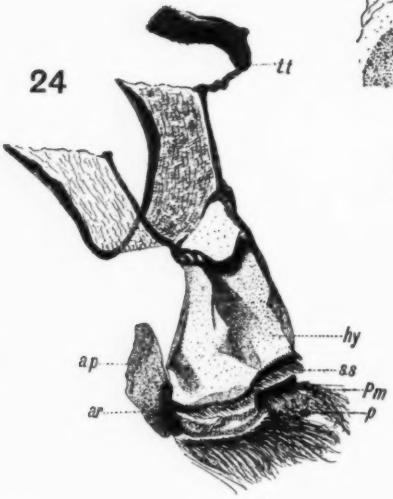

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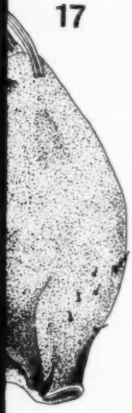

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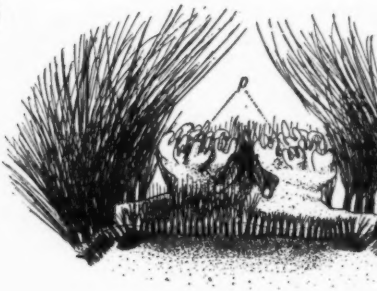

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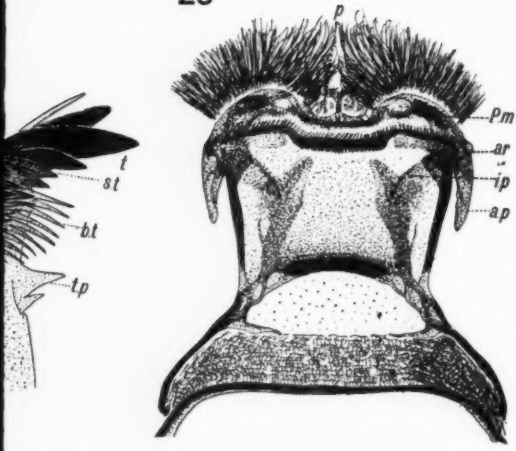

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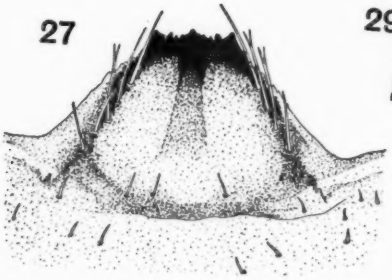

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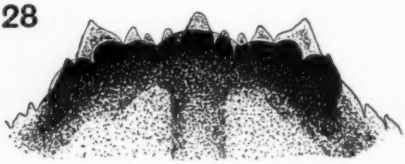
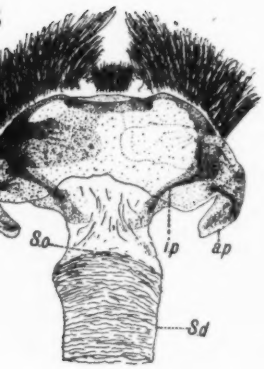
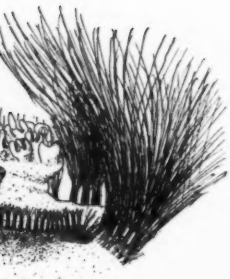
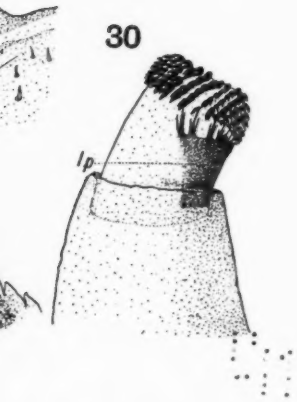


PLATE IX

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